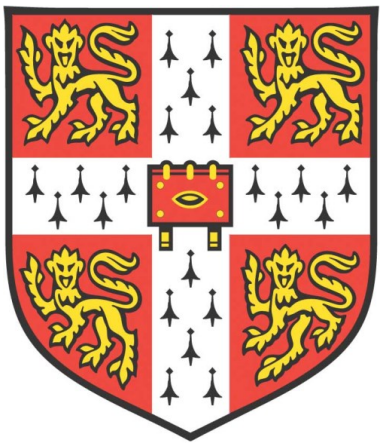
DRIVERS OF VARIATION IN THE MIGRATION AND FORAGING STRATEGIES OF PELAGIC SEABIRDS



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This dissertation is submitted for the degree of Doctor of Philosophy

December 2016

“Not all those who wander are lost”

J.R.R. Tolkien

Wandering albatross, Kaikoura, New Zealand

DECLARATION

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except where specifically indicated in the text.

It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text.

It does not exceed the prescribed word limit for the relevant Degree Committee (School of Biology).

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December 2016

SUMMARY

The ability to move and forage efficiently plays a major role in determining the fate of individuals, and has important implications for population dynamics and ecosystem functioning. Migration is a particular type of movement strategy, whereby animals may travel remarkable distances in order to take advantage of seasonality in resource availability or to avoid arduous winter conditions; however, this can be at a cost in terms of increased mortality. Indeed, anthropogenic threats in non-breeding areas are a major cause of population declines and a better understanding of non-breeding spatial ecology is required in order to advance both ecological theory and conservation management. The recent development of animal tracking technologies, in particular light-based geolocation, has made it possible to track large-scale and long-term movements; however, there are still gaps in our knowledge, such as the links between migratory and reproductive performance, connectivity among populations and the ontogeny of migration strategies. In this thesis, I utilise multi-species and longitudinal datasets from albatrosses and petrels, some of the most mobile species on Earth, to explore the drivers of variation in movements, habitat use and foraging behaviour, and the implications for life history and conservation. In Chapter 1, I provide an overview of the key topics of this thesis. In Chapter 2, I provide quantitative recommendations of minimum sample sizes needed to track pelagic seabird migrations, using data from 10 species. In Chapter 3, I examine between- and within-population differences in the habitat preferences and distributions of albatrosses, including the relative roles of habitat specialization and intra-specific competition. In Chapter 4, I investigate the year-round movement and foraging strategies of petrels living in nutrient-poor environments. In Chapter 5, I examine potential links between foraging behaviour during the non-breeding season and reproductive senescence. In Chapter 6, I explore the ontogeny of foraging behaviour and foraging site fidelity in young albatrosses, shedding light on their "lost years" at sea. Finally, I conclude with a general discussion summarizing main findings and suggesting future work. Overall, my results highlight the complex relationships among individual traits, the environment, movements and foraging behaviour, and population dynamics across the lifespan of individuals, with implications for the conservation of this highly threatened group of species.

ACKNOWLEDGEMENTS

Though my name is on the front of this document, I owe a great deal to a lot of people, without whose contributions, none of this would be possible. Primarily, I have been extremely fortunate to have such attentive, knowledgeable and kind supervisors. Richard Phillips has provided wonderful support through his fantastic insight into all things seabird. I am grateful for his patience, his grammatical perfection, enthusiasm and positive outlook. Despite being incredibly busy, he still found the time to respond to stupid emails with grace. I thank Andrea Manica for his remarkable statistical and ecological insight. He welcomed me into the research group and found time for me when I needed it most. I would also like to thank my advisors, Mike Brooke and Nick Davies, for the useful comments they have provided on progress reports. In particular, since offering me Murphy's petrel data, Mike became a third supervisor and has imparted much useful advice and wisdom.

I was supported financially by a studentship provided by the Natural Environment Research Council (NERC) and by travel and maintenance grants from Darwin College and the Cambridge Philosophical Society, respectively. This thesis is the product of data collection that spans many field seasons, for which I cannot claim credit. John Croxall deserves a lot of recognition for overseeing the research program on Bird Island over many decades and for commencing the long-term tracking, while also providing useful comments on a manuscript. I would like to thank all fieldworkers past and present for their contributions, in particular Jose Xavier and others who helped deploy and retrieve geolocators over many seasons. I am also grateful to the following people who have provided data for various chapters, and insightful comments on manuscripts: Peter Ryan, Joan Navarro and Jacob Gonzalez-Solis.

The following people at the British Antarctic Survey (BAS), provided me with data, analysis tools, lab assistance or advice: Janet Silk processed some of the datasets that feature in this thesis, provided GIS support and valuable contributions to two manuscripts; Andy Wood, Jenny Thomas and Helen Peat assisted with data requests and Louise Ireland with the extraction of environmental variables; Annette Scheffer and Norman Ratcliffe have provided useful answers to questions related to tracking and habitat modelling; Ana Carneiro gave up valuable time in the write-up phase of her PhD to advise me with sample preparation; Paul Geissler helped me find lost samples, and along with Guy Hillyard and Elaine Fitzcharles, supported laboratory work; and Michelle King conducted molecular sexing. Additionally,

Hazel Jackson conducted molecular sexing of Murphy's petrel feathers and Rona McGill has provided advice and assisted with stable isotope analysis, also providing useful comments on a manuscript. Lab work in East Kilbride was funded by a Life Sciences Mass Spectrometry Facility NERC grant. Within the EEG group, Ana Carneiro and Anne-Sophie Bonnet-Lebrun have given great advice on all manner of things. It was a pleasure to work with Lizzie Pearmain and I was particularly lucky to work with such an enthusiastic and hard-working student.

Like my study species, I have been incredibly fortunate to travel to some remote places during my PhD. I would like to thank the following people for providing me with the opportunity to play with seabirds on some amazing islands or for putting up with my company there: Paulo Catry, Maria Dias, Joana Romero, Frank and Buffy Zino, Steve Votier, Beth Clark, Greg and Lisa Morgan and Graeme Taylor. I also thank Alistair Crame, Alison Teague and Nick Cox, for organising a highly enjoyable field course to Svalbard.

I have been extremely lucky to be part of two fantastic student communities; at the Department of Zoology and BAS, and for the latter, Alison Teague deserves much credit. Thanks to members of the EEG for distracting me from work (or perhaps the other way round!), particularly Marius Somveille, Ana Carneiro, Vera Warmuth, Max Gray, Anne-Sophie Bonnet-Lebrun, Dave Daversa and Jolle Jolles; and to other members of the department for happy hours and other regrettable things: Dave Williams, Lizzie Green, Andrew Bladon, Claire Feniuk, Anthony Lamb, Ben Phalan, Sarah Luke and Graham Prescott. Thank you to all students at BAS for a vibrant community and I am particularly grateful to Emma Cross and Emma Garnett for write-up treats. Many thanks also to members of the lively seabird community here past and present, in particular Ana Carneiro, Deborah Pardo, Rocio Moreno, Annette Scheffer, Cat Horswill, Elise Biersma, Hanna Granroth-Wilding, Jamie Cleeland, Jonathan Handley, Sebastián Jiménez, Vicky Warwick-Evans and Maria Dias. Also, to members of Stretten Avenue, Pelham Court and West View, thanks for keeping me sane!

Above all, I want to thank my family for always supporting and believing in me, in particular my siblings, Jonathan, Catherine and Charlie, my aunt Julia and my parents, who fostered in me a love for the natural world that has taken me down this strange path. Finally, Will, through your amazing friendship, enthusiasm and never-ending support, you have reminded me of everything else in life that is important; and I am eternally thankful.

CONTENTS

List of Appendices

EXPLANATORY NOTE ON THE TEXT

Chapters 2 – 6 presented in this thesis were first prepared as manuscripts for submission to peer-reviewed journals. The publication status at the time of writing is indicated at the start of each chapter. Only minor alterations have been made to the text of these chapters in order to improve the readability and overall coherence of the thesis. For this reason, there is a small amount of repetition, particularly in the chapter introductions and methods sections of the thesis.

1 INTRODUCTION

1.1 Animal movement and migration

Animals move in order to find food, mates and to escape from threats such as predators, and these movements are shaped by ecological and evolutionary processes (Nathan et al., 2008). Individuals are expected to make optimal decisions about where to forage in an environment that is often heterogeneous, and in which resources are patchily distributed (Fauchald, 1999). Thus, knowing where and when they preferentially forage and how resource availability drives preferences is important for understanding the distribution of species over time (Johnson, 1980; Guisan and Zimmermann, 2000; Boyce et al., 2002). Ultimately, over the course of many foraging sequences, individual movements can have wide-ranging implications for population dynamics, species conservation and ecosystem function (Stephens and Krebs, 1986; Dingle, 1996; Clobert et al., 2001; Nathan et al., 2008).

Migration represents an extreme type of movement, during which animals may cross ecological barriers in order to track seasonality in resource availability or to avoid harsh winters at higher latitude breeding sites (Newton, 2010). Almost 20% of all species of birds migrate (Kirby et al., 2008), which profoundly changes the structure of communities on a seasonal basis. During their migrations, some species perform astonishing feats of endurance; for example, bar-tailed godwits *Limosa lapponica baueri* take just over a week to fly up to 12,000 km across the Pacific Ocean from Alaska to New Zealand (Gill et al., 2009), Arctic terns *Sterna paradisaea* are able to travel over 80,000 km annually from their breeding sites in the high Arctic to the Southern Ocean and back (Egevang et al., 2010), and in the course of

its 50-year lifespan, an individual wandering albatross *Diomedea exulans* can travel 8.5 million km (Weimerskirch et al., 2013).

Until recent decades, knowledge of the migration of individuals was limited in many species to rare recoveries of a small fraction of the marked population (Alerstam, 1990), or ship-based surveys, which typically provided little information about the actual route taken. The rapid development of tracking technologies, in particular satellite transmitters, GPS and light-based geolocation loggers, coupled with reductions in size and price and improvement in battery capacity have led to their widespread use (Kays et al., 2015). Biologging or biotelemetry enables the remote measurement of data for free-ranging, undisturbed animals as small as 12 g songbirds (DeLuca et al., 2015) and insects (Wikelski et al., 2006); and has revolutionised the field of movement ecology (Nathan et al., 2008). In particular, tracking studies have greatly improved our knowledge of migration routes (e.g. Shaffer et al., 2006) , schedules and stop-over sites (e.g. Guilford et al., 2009), flight and foraging behaviours (e.g. Weimerskirch et al., 2016), habitat associations (e.g. Block et al., 2011), connectivity among populations (e.g. Fraser et al., 2012), links with fitness (Crossin et al., 2014) and overlap with anthropogenic threats (e.g. Fossette et al., 2014).

1.2 Drivers of seabird spatial ecology

Pelagic seabirds provide excellent models for addressing ecological and population-level processes as they are large, conspicuous, long-lived and relatively easy to monitor at their breeding colonies. They are usually wide-ranging, spend the majority of their lives at sea and are top predators of most food webs; and have been considered to be good indicators of the health of marine ecosystems (Piatt and Sydeman, 2007; but see Grémillet and Charmantier, 2010). Pelagic seabirds, and in particular albatrosses and petrels, are among the most threatened groups of birds due to a range of anthropogenic drivers, such as pollution, harvesting, climate change, invasive species at breeding colonies and disease (Croxall et al., 2012, Phillips et al. 2016). Their greatest threat remains incidental mortality in industrial pelagic or demersal longline, trawl or artisanal fisheries in both national and international waters, in part due to their extensive at-sea distributions (Anderson et al., 2011; Jiménez et al., 2014; Phillips et al., 2016).

Traditionally, seabird research focussed on events and processes at the breeding colony. Given that seabirds spend most of their lives at sea, only returning to land to breed, tracking

technologies have been vital in understanding their foraging ecology, including the relationship with the marine environment and overlap with at-sea threats (Burger and Shaffer, 2008; Grémillet and Boulinier, 2009). Seabirds forage in heterogeneous environments, and strategies are dependent on the hierarchical nature of prey distributions in both time and space (Fauchald, 1999; Weimerskirch et al., 2005; Weimerskirch, 2007). Along with other marine predators, they generally target regions of elevated primary productivity arising from physical features, such as shelf breaks, or hydrological processes such as upwellings, frontal zones and eddies (Cotté et al., 2007; Bost et al., 2009; Grecian et al., 2016; Scales et al., 2016). The predictability of prey generally depends on the type of habitat utilised, with shelf-edges more predictable than oceanic habitats, and polar and temperate regions generally assumed to be more predictable than tropical regions (Weimerskirch, 2007).

Whilst seabirds forage in dynamic environments, they appear to be highly faithful to breeding and non-breeding foraging grounds, both within- (Irons, 1998; Hamer et al., 2001; Patrick et al., 2013) and among-years (Phillips et al., 2005; Guilford et al., 2011; Wakefield et al., 2015). They also show repeatable foraging behaviour and diets (Bearhop et al., 2006; Woo et al., 2008; Votier et al., 2010a). Most studies have been conducted on adults (Ceia and Ramos 2015), that have presumably already acquired sufficient knowledge of local areas to make informed decisions about where to forage (e.g. Regular et al., 2013). As a result, studying the resource selection of individuals as juveniles and immatures presents a behavioural 'clean slate' with which to better understand the causes of specializations. Currently however, little is known about the development of migrations and foraging behaviours due to difficulties associated with tracking naïve individuals over long time periods (Hazen et al., 2012). As such, our knowledge of learning processes is limited to studies of short duration, where the foraging performance of younger birds is usually compared to that of unrelated adults (Péron and Grémillet, 2013; Riotte-Lambert and Weimerskirch, 2013).

Tracking studies of seabirds have identified multiple drivers of variation in their movements and foraging strategies during the breeding season. The extent to which they segregate or partition geographic space or resources is specific to sites and species, and is likely to be dependent on levels of inter- and intra-competition (Furness and Birkhead, 1984; Wakefield et al., 2013; Oppel et al., 2015), resource availability (Weimerskirch et al., 1994; Hamer et al., 2007; Wakefield et al., 2014) and intrinsic characteristics such as morphological or physiological constraints (Croxall and Prince, 1980; Ballance et al., 1997), foraging

experience (Fayet et al., 2015) or social dominance (González-Solís et al., 2000; Araújo et al., 2011). A wealth of studies have documented differences in foraging strategies by species (Young et al., 2010; Navarro et al., 2013), colony (Grémillet et al., 2004; Wakefield et al., 2013), sex (Lewis et al., 2002; Phillips et al., 2004a), breeding status (Patrick and Weimerskirch, 2014) and age (Lecomte et al., 2010; Pelletier et al., 2014). Attention has been focussed more recently on the additive effects of individual differences (Ceia and Ramos, 2015).

Outside of the breeding season, birds are no longer constrained by having to return to incubate the egg or provision young and so habitat selection is likely to better reflect intrinsic preferences (Thiebot et al., 2011b). Nonetheless, even in the absence of restrictions imposed by central place foraging, a degree of inter-specific competition and segregation will remain (Quillfeldt et al., 2013; Ratcliffe et al., 2014). Indeed, some studies have found that differences observed in the foraging strategies of birds from different colonies or species during the breeding season are maintained during the non-breeding season (Rayner et al., 2011; Thiebot et al., 2011a, 2012, but see Shaffer et al., 2006; González-Solís et al., 2007). The widespread use of geolocators (detailed below) now makes it possible to build on concepts developed during the breeding season and apply them to the non-breeding season. Consequently, in this thesis, I take advantage of large archival tracking datasets and advances in statistical modelling (detailed below) to explore key questions related to the spatial ecology of seabirds outside the breeding season. I focus on the patterns and drivers of variation in movement and foraging strategies while also demonstrating that variation between individuals can have consequences for population dynamics and is of relevance to their conservation.

1.3 Overview of methods

Geolocators or Global Location Sensors (GLS) loggers record ambient light levels, which can be processed to derive two locations per day estimated from thresholds in light curves (Phillips et al., 2004b). Latitude is generated from day length, and longitude from the time of local midday relative to Greenwich Mean Time and day of the year. The disadvantages of geolocators are that they have low spatial accuracy (average of 186 ± 114 km), latitudes are unreliable for 3 to 4 weeks around equinox periods, and loggers need to be recovered for data to be downloaded (Phillips et al., 2004b; Shaffer et al., 2005). The advantages are that they

are relatively cheap compared with satellite transmitters, and due to low battery requirements, can record for many years (up to c. 4 years). They are lightweight (now < 1 g), allowing attachment to metal leg rings rather than feathers and are suitable for the non-breeding (moult) period (Phillips et al., 2004b), and can be attached to birds weighing < 100 g (e.g. Pollet et al., 2014). Many loggers record saltwater immersion (usually every 3 s) as well as light, storing the sum of positive tests every 10 min, giving a value ranging from 0 (continuously dry) to 200 (continuously wet). A wet bout is usually defined as a 10 min period during which at least one wet event was recorded, and a flight bout as a continuous 10 min period spent entirely dry; from this, information on the daily activity patterns, such as the total time spent sitting on the water (wet) or in flight (dry), can be derived (e.g. Phalan et al., 2007). Additionally, the number of wet bouts can be a useful proxy for the number of landings, which for albatrosses are energetically expensive for albatrosses (Shaffer et al., 2001a; Weimerskirch et al., 2000a). However, as the resolution is limited to 10 min periods, the number of landings are considered to be a minimum value (Lecomte et al., 2010) .

Understanding the factors that influence the selection of particular habitats by animals is of primary concern for ecologists (Johnson, 1980; Boyce et al., 2002). Advances in statistical modelling have made it possible to test ecological hypotheses using large quantities of data (Guisan and Zimmermann, 2000; Aarts et al., 2008), and to model habitat use by incorporating remotely-sensed environmental variables which provide data on oceanographic processes in near real-time (Grantham et al., 2011; Scales et al., 2014). Many modelling techniques exist (Guisan et al., 2002; Elith et al., 2008, 2011), but there is currently no consensus as to which performs best. Different methods are likely to be more appropriate depending on the nature of the question and the temporal and spatial scale of tracking and environmental data (see Oppel et al. 2012 and Scales et al. 2016 for case-specific comparisons). Nevertheless, studies that take into account the availability of suitable habitat, i.e. areas within the movement capabilities of an animal but not those which were selected, have been recommended (Matthiopoulos, 2003; Aarts et al., 2008; Wakefield et al., 2009a). These methods accommodate the non-normal responses of animals to their environments and can control for differences in sampling effort between individuals, in order to draw conclusions at both an individual and a population level (Wood, 2006; Aarts et al., 2008). These methods have proved effective at predicting spatial-usage of populations on a global scale (Wakefield et al., 2011).

While biologging and remotely-sensed oceanography are useful tools to monitor the movements, behaviours and habitat selection of animals, they provide no information on diet. Traditionally, dietary studies relied on methods such as of stomach contents analyses, however they are usually limited to periods when birds are at the breeding colony and they can underestimate digested prey (Barrett et al., 2007). An alternative is the analysis of stable isotopes from tissues samples, with tissue signatures generally reflecting diet during the period of tissue synthesis (Hobson and Clark, 1992). Feathers reflect diet at the period of feather moult, which for many seabirds occurs during the non-breeding season (Bearhop et al., 2000; Cherel et al., 2000). The stable isotopes of interest are carbon and nitrogen, which reflect the habitat of the consumer and the trophic position, respectively (Hobson et al., 1994; Cherel et al., 2006).

1.4 Study sites

This thesis predominantly uses data collected from three species at three sites: grey-headed albatross *Thalassarche chrysostoma* from two colonies: Bird Island, South Georgia (SG) and Marion Island, Prince Edward Islands (PEI) in the Southern Ocean; wandering albatross *Diomedea exulans* from SG; and Murphy's petrel *Pterodroma ultima* from Henderson Island, Pitcairn Islands (PI), in the central South Pacific Ocean (Fig. 1.1, 1.2). Tracking data from grey-headed and wandering albatross have been supplemented by data from a further eight seabird species breeding on SG for a multi-species comparison in Chapter 2.

Most of the data for Chapters 2, 3, 5 and 6 were collected by the British Antarctic Survey on subantarctic Bird Island, part of the South Georgia archipelago (54°00'S, 38°03'W) within the United Kingdom Overseas Territory (UKOT) of South Georgia and the South Sandwich Islands. The island lies 300 km south of the Antarctic Polar Front in the southwest Atlantic Ocean and is 4.8 km long and max. 800 m wide, yet hosts millions of pairs of breeding seabirds, in one of the world's densest aggregations (Croxall and Prince, 1980). The island has been the subject of long-term monitoring programs since the 1950s (Tickell et al., 1965; Croxall et al., 1990). It is a globally important breeding station for many species, including both grey-headed (See Appendix 2) and wandering albatrosses; both species are experiencing major declines and are a conservation priority (Phillips et al., 2016). Data were also collected from Marion Island, a subantarctic Island in the Prince Edwards Islands (46°54' S, 37°45' E) (Fig. 1.1), part of the South African Overseas Territories. The island lies 300 km north of the

Antarctic Polar Front in the southwest Indian Ocean, is 25.0 km long and 16.7 km wide, and is also a major breeding site for both albatross species. Data used in Chapter 4 were collected from another UKOT, Henderson Island of the Pitcairn Islands chain (24°20' S, 128°20' W) (Fig. 1.1). The island is a raised coral atoll in the South Pacific Ocean, is 9.6 km long and 5.1 km wide and is a major breeding site for gadfly petrels. In contrast to Bird Island and Marion Island where there are long-term monitoring studies, data were collected opportunistically over two field seasons, with logistical assistance from the Royal Society for the Protection of Birds (RSPB) rat eradication program.

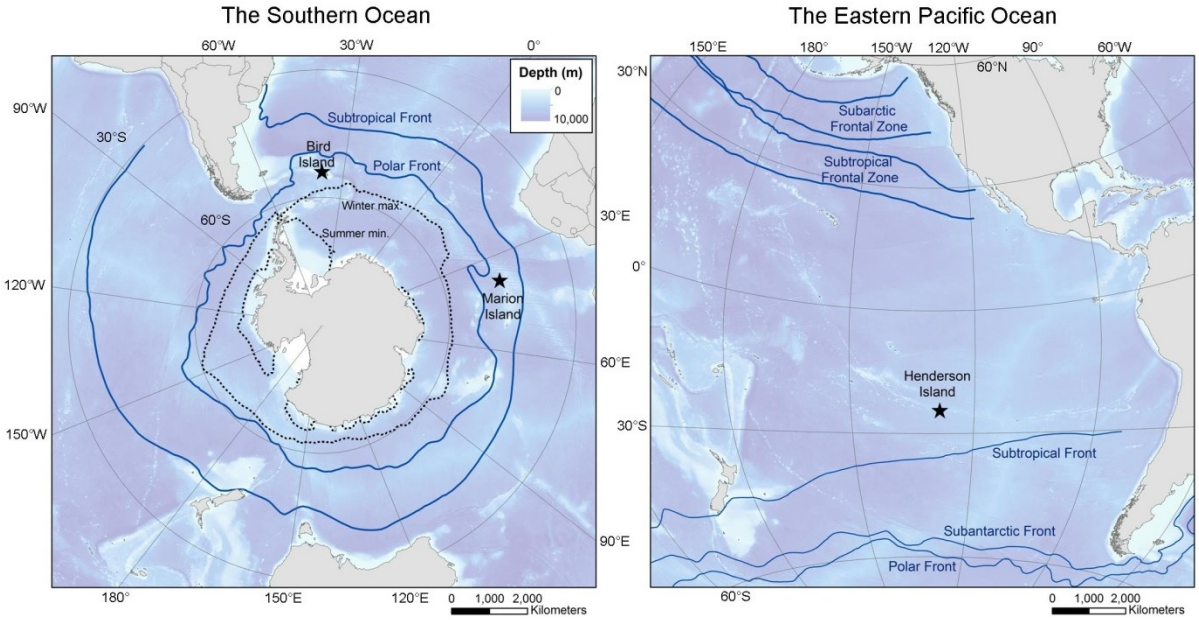


Figure 1.1. Maps of the Southern Ocean and the Eastern Pacific Ocean, showing the three study sites. Fronts in Southern Ocean are from the Australian Antarctic Division (AAD) and fronts in North Pacific are spring and autumn positions of Subtropical and Subarctic fronts based on isotherms from Hyrenbach et al. 2002. The average winter maximum and summer minimum sea ice extents (> 15% concentration) are shown as dotted lines for the period 1981-2010.

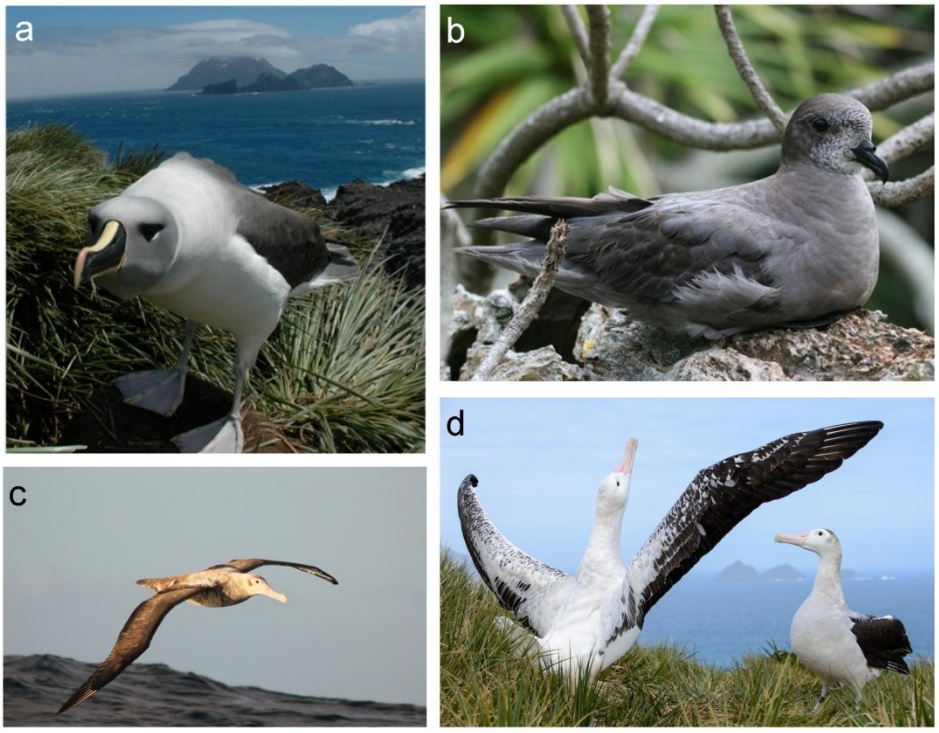


Figure 1.2. The main study species: a) grey-headed albatross *Thalassarche chrysostoma* on Bird Island, b) Murphy's petrel *Pterodroma ultima* on Henderson Island, c) immature wandering albatross *Diomedea exulans* off the coast of Brazil, and d) courtship of wandering albatrosses on Bird Island. Photo credits: a) Richard Phillips, b) Michael Brooke, c) Dimas Gianuca, and d) Alastair Wilson.

The regions surrounding the study sites featured in this thesis have contrasting oceanography. The Southern Ocean is highly seasonal, with regions of high productivity around South Georgia and the Antarctic Peninsula, particularly during the austral summer. The region around Marion Island is an area of high frontal and eddy activity, created by the Agulhas Return Current (Nel et al., 2001). In contrast, due to its remoteness, relatively little is known about the South Pacific; however the South Pacific Gyre exhibits relatively low seasonality and is considered to be an "ocean desert", one of the least productive marine regions on Earth (Claustre and Maritorena, 2003).

1.5 Study species

Many seabirds, and the Procellariiformes (albatrosses and petrels) in particular, possess unusual life history characteristics compared to most terrestrial species, but grey-headed and wandering albatross are some of the most *k*-selected even of these species. They exhibit delayed sexual maturity, with age of first reproduction around 10-12 years (Tickell, 2000),

and have prolonged breeding seasons; for wandering albatross, the period from arrival at the colony to last visit to the chick lasts >380 days (Tickell, 1968). Both are quasi-biennial breeders and have a particularly low breeding frequency; although grey-headed albatrosses are able to breed annually with a breeding season lasting 6-7 months - most birds from South Georgia (99%) take a year off following a successful breeding attempt (Ryan et al., 2007). These species have high survival under natural conditions, and are amongst the longest-lived of any wild birds (Croxall et al., 1990; Prince et al., 1994). They forage predominantly in oceanic waters and, during the breeding season, frontal regions appear to be very important for grey-headed albatross, and to some extent for wandering albatross, likely related to the distribution of their preferred prey; cephalopods and fish (Rodhouse et al., 1990; Xavier et al., 2003a, 2003b; Catry et al., 2004). During the non-breeding season, both species have a circumpolar distribution, and are among the most wide-ranging of any seabird species (Croxall et al., 2005; Weimerskirch et al., 2015).

In contrast, while gadfly petrels *Pterodroma* spp. are known to feed far from continental shelves (Warham, 1990), little is known about the foraging habits of many species, including Murphy's petrel. This species has one of the longest incubation shifts of any seabird (Warham, 1990), thought to be related to low food availability in the region and so are presumed to conduct foraging trips to distant areas (Brooke, 1995), where they feed on mesopelagic squid (Imber et al., 1995), yet no study had, until now, investigated their movements. They are also presumed to migrate to the North Pacific during their non-breeding season, based on rare sightings (Bartle et al., 1993).

1.6 Thesis aims and structure

The major aims of this thesis are:

- to quantify habitat use and selection by pelagic seabirds in contrasting oceanic environments.
- to determine the drivers of within-species variation in foraging strategies, focussing on population, sex, breeding status, age and individual differences.
- to characterize the development of movements and foraging behaviour across juvenile and immature life-stages.

- to consider the implications of variation in foraging strategies for life history theory and for marine spatial planning and conservation.

In **Chapter 2**, I assemble a remarkably comprehensive tracking dataset detailing the non-breeding movements of 305 individuals from 10 pelagic seabirds. I use these data to investigate the relationship between sample size and home range area, and determine the minimum number of individuals required to predict important areas for populations. I also investigate the role of individual and annual variability in movement strategies on minimum sample sizes required. The recommendations from this study aim to assist researchers and practitioners that use biologging to inform conservation outcomes.

In **Chapter 3**, I investigate the relative roles of intrinsic (population, previous breeding outcome, sex) and extrinsic (habitat availability and intra-specific competition) drivers on the spatial distribution of non-breeding grey headed albatrosses. Firstly, I describe and compare the migration characteristics of 66 adults tracked with geolocators from two distant populations, and investigate the incidence of spatial segregation between and within populations. Secondly, I combine tracking data with remotely-sensed oceanography within a use-availability habitat modelling framework, to determine the relative contributions of environmental and colony-level parameters to observed distribution patterns. Thirdly, I compare habitat preferences between birds from different populations, and of different previous breeding outcome (successful or unsuccessful) and sex, to determine the drivers of segregation between groups. This study provides insight into the habitat preferences of pelagic seabirds during the non-breeding season, including how they might interact or compete within and among populations. I discuss my results in the context of population ecology, with wider implications of large-scale spatial segregation for the management of this and other threatened species.

In **Chapter 4**, I investigate the hitherto unknown year-round movements and foraging ecology of 18 Murphy's petrels, tracked with geolocator-immersion loggers over two years. I detail the year-round foraging strategies that petrels use to exploit or, to some extent, avoid one of the least productive marine habitats on Earth, the South Pacific Gyre. These results have implications for the study of seabirds in unproductive marine environments, in particular gadfly petrels, a poorly understood group of species.

In **Chapter 5**, I investigate the effect of age and sex on the foraging ecology of non-breeding wandering albatrosses, and subsequent links with fitness, using a cross-sectional dataset of 82 adults tracked with geolocator-immersion loggers over two non-breeding seasons. I link behavioural variables that show an age effect to subsequent reproductive performance, testing the prediction that non-breeding foraging behaviour would influence reproductive senescence. These results emphasize the neglected role of the non-breeding season in studies of senescence in wild populations.

In **Chapter 6**, I use a longitudinal dataset of wandering albatrosses tracked from fledgling, through immaturity, and for some birds, as non-breeders following recruitment into the breeding population, to examine the ontogeny of foraging behaviour and migratory performance. Over a 13-year period, 22 birds were tracked with geolocator-immersion loggers, for up to 8 years per individual. I investigate the post-fledging dispersal of juveniles and the extent to which individual variation is maintained throughout their early lives. I examine the degree to which birds are faithful to particular areas and how foraging site fidelity and foraging behaviour change with age. This study provides remarkable insight into the "lost years" of seabirds, emphasizing the potential roles of individual experience and site familiarity in shaping lifetime migration strategies. These results have important implications for the evolution and maintenance of pelagic migrations in a rapidly changing climate.

In **Chapter 7**, I bring together the main findings of my thesis, and the implications for the conservation of pelagic species and also for the study of animal migration and life history theory. I also suggest future work that could arise from this thesis.

1. Introduction

2 How many tags? Minimum sample sizes and implications for identifying marine protected areas for non-breeding seabirds

2.1 Introduction

Many marine vertebrate populations have declined in recent decades due to the combined effects of anthropogenic stressors, including harvesting, competition with fisheries, incidental mortality (bycatch), climate change, pollution and invasive species (Halpern et al., 2008; Croxall et al., 2012; Phillips et al., 2016). Managing these threats can be challenging as many marine taxa undertake long-distance migrations, crossing national jurisdictions to take advantage of seasonally productive areas, including in the high seas (Phillips et al., 2005; Block et al., 2011; Louzao et al., 2012). Advances in archival and satellite tracking technology have revolutionized our understanding of their ocean basin-scale movements, habitat requirements and fine-scale behaviours (Pinaud and Weimerskirch, 2007; Block et al., 2011), and tracking data have become increasingly important for identifying key habitats for potential designation as Marine Protected Areas (MPAs) (Maxwell et al., 2011; Lascelles et al., 2016). Foraging habitats for pelagic species are often linked to complex oceanographic processes (Wakefield et al., 2009a), and studies that integrate animal-borne telemetry with remotely sensed environmental data are increasingly important as key habitats may shift

geographically over short or long time-scales (Weimerskirch et al., 2012; Clay et al., 2016, Chapter 3).

If tracking data are to be used for the identification of important areas for conservation, the aim should be to predict utilization hotspots of a population rather than just the sampled individuals (Lindberg and Walker, 2007; Raymond et al., 2014; Lascelles et al., 2016). However, scaling up from individual tracks can be challenging (Block et al., 2011; Gutowsky et al., 2015). Marine predators often exhibit within-species variation in foraging strategies specific to population (Grémillet et al., 2004), sex (Phillips et al., 2004a), breeding status (e.g. Clay et al., 2016; Chapter 3), age class (e.g. Votier et al., 2010), and individual specialisation (Ceia and Ramos, 2015). Sampling should therefore be sufficient to capture this level of variation (Lindberg and Walker, 2007).

Over recent decades, although the size and cost of tracking devices have decreased substantially, research often remains constrained by limited funding or logistics, and there are also increased ethical concerns about negative effects of devices (Burger and Shaffer, 2008). Previous studies have emphasised the importance of sampling regime and study design (Börger et al., 2006; Hebblewhite and Haydon, 2010; Fieberg and Börger, 2012), and samples of at least 20 – 30 individuals have been recommended for marine predators (Schofield et al., 2013; Hays et al., 2016). Recent studies of sampling effects in seabirds tracked during breeding have found that the required number of individuals depends on the number of trips included in the sample (Soanes et al., 2013), and that variability among individuals and years can greatly influence interpretation (Bogdanova et al., 2014; Gutowsky et al., 2015; Warwick-Evans et al., 2016). Yet, logistical constraints mean that most tracking samples cover a limited number of years (but see Bogdanova et al., 2014), and it remains unclear whether the common practice of pooling multiple years of tracking data in kernel analysis (Delord et al., 2014) is sufficient for identifying predictably important areas for conservation, such as areas of overlap with fisheries (Jiménez et al., 2016).

While a thorough assessment of the representativeness of a tracking sample has been identified as an important step in marine spatial planning (Delord et al., 2014; Lascelles et al., 2016), it is far from routine. This study expands upon attempts to quantify the representativeness of tracking samples of a handful of seabird species during the breeding season (Soanes et al., 2013), to provide a robust assessment of sampling design in a major seabird community during the non-breeding season. During non-breeding, seabirds are no

longer constrained by having to return to incubate the egg or provision young, and individuals may disperse over much wider and more distinct areas than during breeding (e.g. Guilford et al. 2011; Dias et al. 2012; Clay et al. 2016; Chapter 3). As a result of greater potential for within-population variation in movements, it has been suggested that more individuals would need to be tracked (Soanes et al. 2013). A recent study of North Pacific albatrosses provides tentative support for this theory; the area occupied by the population of over-wintering birds appeared to reach an asymptote at larger sample sizes (or did not asymptote) than during breeding (Gutowsky et al. 2015). Despite this, our understanding of sampling design remains limited as comparisons have been made between ecologically similar species (Orben et al. 2014, Gutowksy et al. 2015).

Here, I compile available data for ten pelagic seabird species, ranging from small petrels to large albatrosses and including a diverse suite of migratory strategies, tracked from Bird Island, South Georgia (Table 2.1). The aim of this study is to provide researchers and conservation managers with quantitative, species-specific estimates of minimum sample sizes required to capture individual and annual variation within populations in core and general use areas during the non-breeding season. By calculating the size and location of foraging areas for an increasing number of individuals, it is possible to predict the size of foraging areas used by the entire population (Soanes et al., 2013; Warwick-Evans et al., 2016). Within this framework, I provide recommendations for predicting important areas for a population in terms of 1) minimum number of individuals required, 2) the influence of individual variation in movement strategies, and 3) variation between years.

2.2 Methods

2.2.1 Data collection

Fieldwork was carried out between 1999 and 2012 on Bird Island, South Georgia (54°00’S, 38°03’W), which hosts globally important populations of many seabird species (Table 2.1). Ten species were tracked with geolocators (British Antarctic Survey, Cambridge, UK) for at least one non-breeding season: wandering *Diomedea exulans* (WA), black-browed *Thalassarche melanophris* (BBA), grey-headed *T. chrysostoma* (GHA) and light-mantled sooty albatross *Phoebetria palpebrata* (LMSA), northern *Macronectes halli* (NGP) and southern giant *M. giganteus* (SGP), and white-chinned *Procellaria aequinoctialis* (WCP) and

blue petrel *Halobaena caerulea* (BP), Antarctic prion *Pachyptila desolata* (AP) and brown skua *Stercorarius antarcticus lonnbergi* (BS). Deployment details are already published for eight species (Croxall et al., 2005; Phillips et al., 2005, 2006; González-Solís et al., 2008; Quillfeldt et al., 2013; Navarro et al., 2015; Carneiro et al., 2016; Clay et al., 2016, Chapter 3); see Appendix 1 for WA and LMSA. Four (AP, BBA, BS and LMSA) and one (WA) species were tracked for two and three non-breeding seasons, respectively, providing a total of 16 species-year combinations (Table 2.2).

Table 2.1. Habitat preferences, IUCN status and population sizes of species considered in this study. Population sizes are the estimated number of breeding pairs from the South Georgia archipelago.

Species and abbreviation	Scientific name	Habitat preferences	IUCN status	South Georgia population	% global population[1]
Antarctic prion (AP)	*Pachyptila desolata*	O	LC	22,000,000[2]	> 85
Black-browed albatross (BBA)	*Thalassarche melanophris*	SH + SE	EN	74,300[3]	12
Blue petrel (BP)	*Halobaena caerulea*	O	LC	70,000[2]	5
Brown skua (BS)	*Stercorarius antarcticus*	O	LC	2,000[1]	10 - 20
Grey-headed albatross (GHA)	*Thalassarche chrysostoma*	O	EN	47,700[3]	40
Light-mantled sooty albatross (LMSA)	*Phoebetria palpebrata*	O	NT	5,000[4]	20
Northern giant petrel (NGP)	*Macronectes halli*	O + SE	LC	17,200[1]	45
Southern giant petrel (SGP)	*Macronectes giganteus*	O + SE	LC	8,700[1]	15
Wandering albatross (WA)	*Diomedea exulans*	O	VU	1,550[3]	12
White-chinned petrel (WCP)	*Procellaria aequinoctialis*	SH + SE	VU	900,000[5]	50

[1]Clarke et al., 2012, [2]Prince & Croxall 1983, [3]Poncet et al. 2006, [4]Thomas, Croxall & Prince 1983, [5]Martin et al. 2009 Habitat preferences: O = oceanic, SH = continental shelf, SE = continental shelf edge. IUCN status: LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered

2.2.2 Home range analysis

Light data were processed using MultiTrace Geolocation (Jensen Software Systems) or BASTrak software (British Antarctic Survey, Cambridge, UK), providing two positions per day with a mean error 186 ± 114km (Phillips et al., 2004b). I excluded locations with interruptions around sunrise and sunset, and periods around the equinox (3 to 4 weeks), when latitude cannot be estimated reliably. For each individual, the non-breeding period was defined as the time from the start of outward migration to return to the breeding grounds, and was derived from location and immersion data.

The concept of the home range is that it represents the area used by an individual over a given time period (Burt, 1943). Home ranges can be estimated in many ways, but the most widespread method generates utilization distribution (UD) kernels (Worton, 1989), and is straightforward to implement, generally robust to changes in spatial resolution and performs as well as more complicated approaches (Börger et al., 2006; Tancell et al., 2012). For tracking data with high location uncertainty, a smoothing factor representing the average accuracy of location estimates is recommended (Fieberg and Börger, 2012), and so I selected a value of 200 km, and used a cell size of 50 km (Phillips et al., 2004b). I created population UDs by merging individual UDs, assigning them equal weighting. To best enable comparisons with other studies, I consider the 50% and 95% UDs as core and general use areas of a population, respectively (Lascelles et al., 2016).

2.2.3 Sample size predictions

I carried out a resampling approach whereby I calculated the home range area for an increasing number of individuals, selected at random 1,000 times, without replacement. I fitted a range of non-linear models to the resampled data to best determine the relationship between sample size and home range area for each species-year combination. These models were used to predict home range area for a range of hypothetical sample sizes, to control for the fact that observed sample sizes varied among groups. Previous studies indicated that the area occupied reaches an asymptote once a certain number of individuals are included (Hindell et al., 2003; Soanes et al., 2013), and so I considered four asymptotic relationships; the two- and three-parameter Michaelis-Menten and the two- and three-parameter asymptotic exponential models within the R package *drc* (Ritz and Strebig, 2015) (see Appendix 1 for details). I carried out a sensitivity analysis to determine which models fitted the resampled

data best, by ranking models according to Akaike Information Criterion (AIC) values (Table A1.1 in Appendix 1).

For each species-year combination, I extrapolated the home range area for a predicted population size (Fig. A1.2 in Appendix 1). I chose not to extrapolate home range areas to observed population sizes, which for some species are in the order of millions of breeding pairs (Table 2.1), and instead chose a 'colony' size of 50 individuals, which is generally the upper end of sample sizes of birds tracked in a particular breeding stage in any given year. In order to determine the sensitivity of the predictions to 'colony' size, I also extrapolated home range area to 100 and 1,000 individuals. I determined that sufficient individuals were tracked at a cut-off of 95% of the core and general use areas predicted for 50 individuals (see Fig. A1.2 in Appendix 1 for details), which appeared to be an appropriate cut-off (Fig. 2.2), and refer to these predicted sample sizes as minimum sample sizes throughout. Similarities or differences are quantified based on the overlap of 95% confidence intervals (CI) around modelled predictions.

2.2.4 Factors influencing sampling design

For the majority of species tracked over multiple years, an indepedent sample of individuals was selected each year, yet for some species, the same individual featured more than once. As individuals are known to be faithful to wintering sites between years (e.g. Phillips et al., 2005; Guilford et al., 2011), species with repeatedly tracked individuals might exhibit less annual variation than those with a different selection of individuals. As a result, I implemented a sub-sampling approach to investigate the sensitivity of predicted minimum sample sizes to the number and chance selection of individuals in tracking samples. For species where the same individual was tracked for more than one year, I created two random sub-samples from the larger sampling year that matched the sample size of the smaller sampling year: 1) including all individuals tracked repeatedly, and 2) excluding those individuals. I compared predicted minimum sample sizes for the sub-sampled datasets with those for the full datasets from both years to determine if differences were due to sample size or the selection of individuals in the samples. Further details are given in Appendix 1.

Minimum sample sizes might vary according to habitat type, and so results were compared among species that typically utilise either oceanic or continental shelf waters during the non-breeding season (Table 2.1). Additionally, I modelled hypothesized drivers of predicted

minimum sample sizes: the observed sample size, the population home range area of the full sample, and individual variability based on a metric of between-individual differences for each species-year combination. I chose the home range (HR) method within the *adehabitat* package in R (Calenge, 2006), which determines the percentage of overlap between two areas, to calculate overlap between individuals at the 50% and 95% isopleth level. Following (Fieberg and Kochanny, 2005):

$$HR_{i,j} = A_{i,j}/A_i \quad (1)$$

$HR_{i,j}$ is the proportion of the home range of animal i overlapped by animal j, A_i is the area of i's home range and $A_{i,j}$ is the area of overlap between the two animals' home range. In order to convert this into an index of individual variability, $IV_{i,j}$, I used the following equation:

$$IV_{i,j} = 1 - \left(\frac{HR_{i,j} + HR_{j,i}}{2}\right) \quad (2)$$

For each species-year, I calculated $IV_{i,j}$ for all pairwise combinations of individuals and extracted the median. I ran generalized linear mixed models for core and general use areas separately within the *lme4* package in R (Bates et al., 2015), with minimum sample size as a response variable, population home range area and the observed sample size as fixed effects and the random effect of species to control for multiple years of tracking. Population home range areas were log-transformed to improve the spread of data values and the interaction between home range area and observed sample size was included as larger sample sizes generally lead to larger home ranges (Fig. 2.1). I used AIC values to rank all possible model combinations according to their degree of parsimony; where multiple models were within 2 AIC units of the best supported model, the most parsimonious model was chosen (Burnham and Anderson, 2004; Arnold, 2010). All analyses were conducted in R v. 3.1.1 (R Core Team, 2014). Areas are reported in millions of km^2 and means are given ± standard deviation (SD), unless reported otherwise.

2.3 Results

I mapped the non-breeding distributions of 305 individuals from 10 species, for up to 3 non-breeding seasons (Table 2.2). I fitted four asymptotic functions to 16 species-year datasets, of which the 3-parameter Michaelis Menten model performed best for 12 (75%) combinations for core areas, and 14 (88%) combinations for general use areas (Table A1.1 in Appendix 1).

This model was therefore adopted for all datasets in order to provide a standardized method for prediction and comparison of minimum sample sizes. The fitted asymptotic curves appeared to match observed relationships well in most cases (Fig. 2.1). Notable exceptions were for species with low sample sizes, e.g. AP in 2011 (Fig. 2.1b) and for BBA in both years, where models over-predicted core areas at low sample sizes, but under-predicted general use areas at larger sample sizes (Fig. 2.1)

2.3.1 Predicted minimum sample sizes

Predictions from models indicated large variability between species in the percentage of predicted home ranges represented by observed samples, and thus, the minimum sample sizes predicted (Table 2.2, Fig. 2.2). Fewer individuals were needed to predict core rather than general use areas (Paired *t*-test, t_{15}=-5.5, $P < 0.001$); for 12 (75%) species-year combinations, observed samples sizes were sufficient to predict core population areas, whereas for only 6 (38%) combinations, were sample sizes sufficient to predict general use areas (Table 2.2). The minimum number of individuals required to represent core areas ranged from 3 (CI: 3 – 4) birds for SGP, to 22 (CI: 22 – 22) birds for WA in 2004, and for general use areas from 10 (CI: 10 – 10) birds for NGP, to 27 (CI: 26 – 27) birds for BBA in 2002. For all species and year combinations, a median of 11 and 19 (mean: 11 ± 6 and 19 ± 6) individuals were required to represent core and general use areas, respectively. There were no significant differences in the minimum sample sizes for species that target the continental shelf or shelf-break (mean: 8 ± 5) compared with oceanic species (mean: 11 ± 5) (Table 2.1), for either core (two-sample *t*-test, $t_{7.1} = -1.2$, $P = 0.28$) or general use areas (two-sample *t*-test, $t_{6.2} = -0.7$, $P = 0.51$). Additionally, although projecting to a larger 'colony' size increased the minimum sample required (Table A1.2, Fig. A1 in Appendix 1), the difference between predictions for 50, 100 and 1,000 individuals was not significant for core areas (mean for 50: 11 ± 5, 100: 12 ± 7 and 1,000 individuals: 14 ± 9; One-way repeated measures ANOVA, $F_2 = 1.0$, $P = 0.4$), but was significant for general use areas (mean for 50: 19 ± 6, 100: 24 ± 8 and 1,000 individuals: 31 ± 15; One-way repeated measures ANOVA, $F_2 = 6.7$, $P = 0.003$).

Table 2.2. Observed and predicted minimum sample sizes, and core (50% UD) and general use (95% UD) home range (HR) areas (millions of km^2) for ten species of seabird tracked during the non-breeding season with geolocators from Bird Island, South Georgia.

Species	Year	Sample size	Individual HR area		Population HR area		Minimum number predicted		Predicted HR area at required sample	
			50%	95%	50%	95%	50%	95%	50%	95%
AP	2010	9	0.8 ± 0.2	3.6 ± 0.8	1.0	5.4	6 (6 – 7)	12 (11 – 13)	1.0 (1.0 – 1.0)	5.5 (5.5 – 5.6)
	2011	6	0.6 ± 0.2	3.7 ± 2.1	1.1	5.8	11 (10 – 12)	13 (10 – 15)	1.2 (1.1 – 1.2)	6.1 (5.9 – 6.3)
BBA	2002	25	0.9 ± 0.3	7.8 ± 3.1	1.4	20.9	7 (7 – 7)	27 (26 – 27)	1.3 (1.3 – 1.3)	20.9 (20.7 – 21.0)
	2003	24	1.0 ± 0.4	7.8 ± 2.7	1.5	18.0	6 (6 – 6)	21 (21 – 22)	1.4 (1.4 – 1.4)	17.7 (17.6 – 17.8)
BP	2011	9	1.6 ± 1.2	6.6 ± 4.8	1.7	15.6	5 (3 – 9)	24 (23 – 25)	1.7 (1.6 – 1.7)	17.9 (17.6 – 18.3)
BS	2002	6	0.7 ± 0.2	3.0 ± 0.6	1.2	4.6	11 (10 – 11)	12 (11 – 12)	1.3 (1.3 – 1.3)	4.9 (4.9 – 5.0)
	2012	19	1.0 ± 0.4	4.3 ± 1.5	2.3	11.9	14 (13 – 14)	23 (23 – 23)	2.2 (2.2 – 2.2)	12.0 (11.9 – 12.1)
GHA	1999-2000	22	2.9 ± 1.1	18.7 ± 10.0	6.2	46.6	16 (15 – 16)	26 (25 – 26)	6.1 (6.1 – 6.1)	47.0 (46.8 – 47.3)
LMSA	2004	25	2.3 ± 0.7	9.3 ± 3.1	3.6	17.9	8 (8 – 8)	16 (16 – 17)	3.4 (3.4 – 3.4)	17.4 (17.3 – 17.4)
	2005	11	2.0 ± 0.4	11.8 ± 3.8	2.6	20.0	7 (7 – 8)	15 (14 – 16)	2.6 (2.6 – 2.6)	20.5 (20.3 – 20.6)
NGP	2000	25	1.2 ± 0.3	5.9 ± 1.2	1.7	8.4	7 (7 – 7)	10 (10 – 10)	1.6 (1.6 – 1.6)	8.1 (8.1 – 8.1)
SGP	2000	29	1.2 ± 0.5	7.3 ± 3.1	1.4	14.4	3 (3 – 4)	16 (16 – 16)	1.4 (1.4 – 1.4)	13.9 (13.8 – 13.9)
WA	2004	15	2.9 ± 1.4	19.5 ± 8.0	7.8	48.7	22 (22 – 22)	21 (21 – 22)	8.1 (8.1 – 8.2)	50.3 (50.1 – 50.5)
	2008	37	2.6 ± 1.6	18.1 ± 7.6	6.7	52.5	18 (18 – 18)	23 (23 – 23)	6.4 (6.4 – 6.4)	50.7 (50.6 – 50.7)
	2009	33	2.7 ± 1.5	15.9 ± 9.0	5.3	46.7	14 (14 – 14)	26 (26 – 27)	5.2 (5.1 – 5.2)	45.4 (45.3 – 45.6)
WCP	2003	10	0.8 ± 0.2	3.7 ± 0.7	1.6	7.3	14 (14 – 15)	19 (18 – 19)	1.7 (1.7 – 1.7)	7.8 (7.7 – 7.8)

Areas are mean ± SD, and minimum sample sizes and areas are shown with 95% confidence intervals in parentheses. Predictions are for a 'colony' size of 50 individuals. AP = Antarctic prion, BBA = black-browed albatross, BP = blue petrel, BS = brown skua, GHA = grey-headed albatross, LMSA = light-mantled sooty albatross, NGP = northern giant petrel, SGP = southern giant petrel, WA = wandering albatross, WCP = white-chinned petrel.

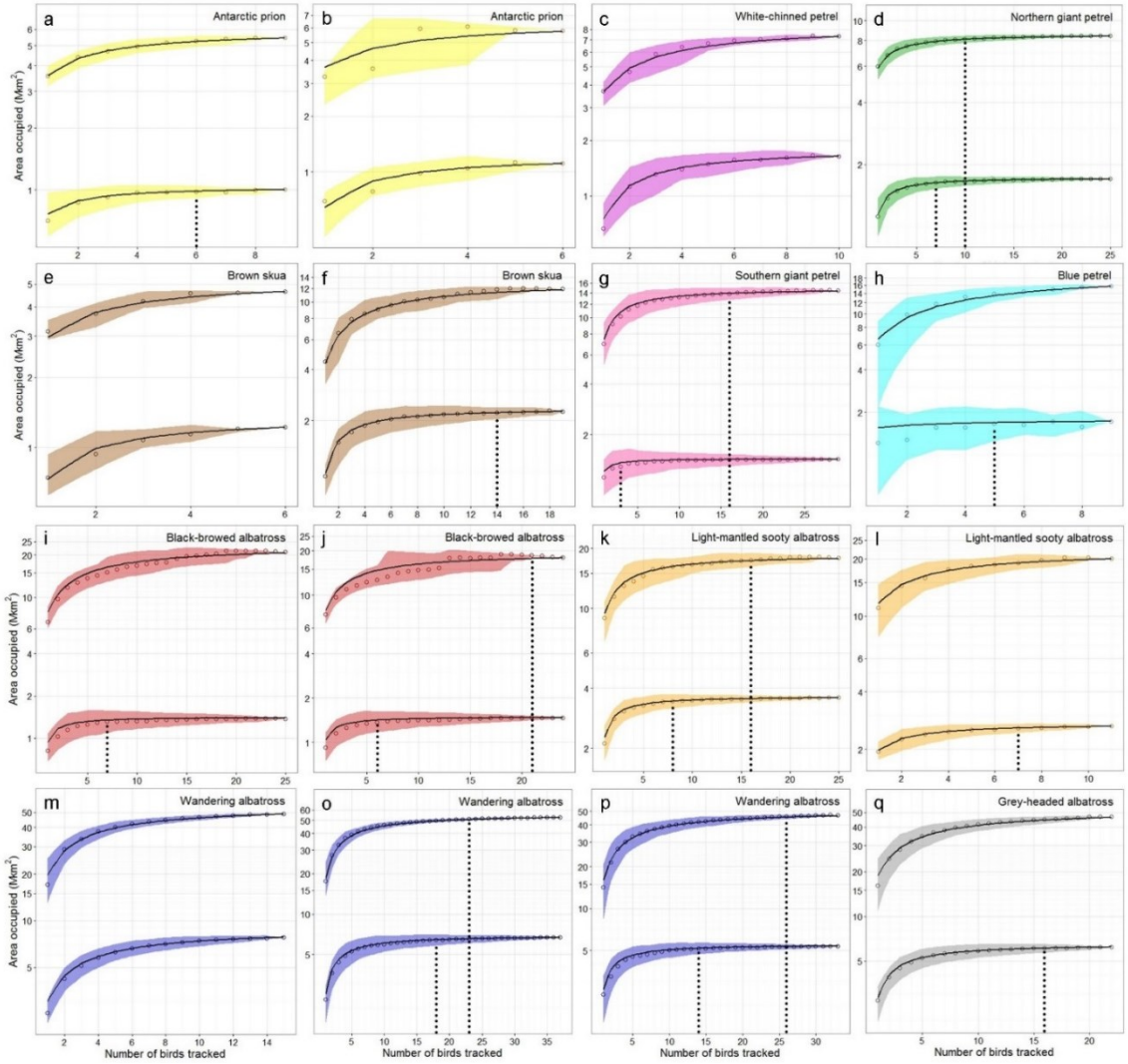


Figure 2.1. Home range area (millions of km^2) as a function of sample size for ten species of seabird tracked during the non-breeding period with geolocators from Bird Island, South Georgia: a) Antarctic prion (AP) in 2010, and b) in 2011, c) white-chinned petrel (WCP) in 2003, d) northern giant petrel (NGP) in 2000, e) brown skua (BS) in 2002, and f) in 2003, g) southern giant petrel (SGP) in 2000, h) blue petrel (BP) in 2011, i) black-browed albatross (BBA) in 2002, and j) in 2003, k) light-mantled sooty albatross (LMSA) in 2004, and l) in 2005, m) wandering albatross (WA) in 2004, o) in 2008, and p) in 2009, and q) grey-headed albatross (GHA) in 1999-2000. In each plot, fitted asymptotic relationships (black lines), and medians (coloured, open circles) and 25% and 75% quantiles (coloured, shaded polygons) of 1,000 resampled iterations are shown for the general use (95% UDs, top) and core (50% UDs, bottom) areas. To show trends for both core and general use areas, the y-axis has been log-transformed and the scale

varies according to the species. Where predicted minimum sample sizes are lower than observed tracking sample sizes, they are shown by a dotted vertical line.

2.3.2 Annual and individual variability

For the most part, core distributions of the five species tracked for more than one non-breeding season did not vary between years (Fig. 2.3). Exceptions were for LMSA, where the South Georgia region was used to a greater extent by the larger sample of birds tracked in 2004, and by WA tracked in 2009, when fewer individuals migrated to waters around New Zealand. Minimum sample sizes for core and general use areas varied among years for 4 (AP, BBA, BS and WA) and 3 (BBA, BS and WA) species, respectively. For some species it was apparent that differences in predicted minimum sample sizes among years were influenced by the chance selection of particular individuals in the sample and by the size of the sample, but these differences did not appear to influence general among-species patterns (see Appendix 1).

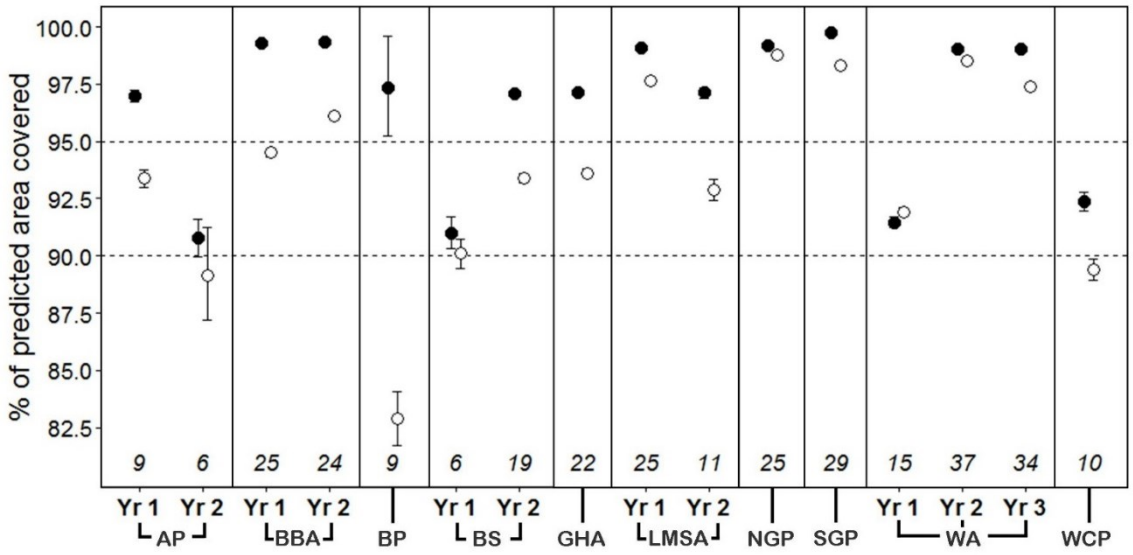


Figure 2.2. Percentage of the predicted home range area for a population size of 50 individuals that is covered by the home range of the observed tracking sample for each species-year combination (multiple years for the same species indicated as Yr1 - Yr3). Predictions are shown with confidence intervals for core (50% UDs, filled circles) and general use (95% UDs, open circles) areas, where large enough to be visible. Sample sizes for each group are indicated at the bottom of the plot and dashed horizontal lines indicate 90% and 95% cut-offs. See Appendix 1 for predictions for larger 'colony' sizes.

AP = Antarctic prion, BBA = black-browed albatross, BP = blue petrel, BS = brown skua, GHA = grey-headed albatross, LMSA = light-mantled sooty albatross, NGP = northern giant petrel, SGP = southern giant petrel, WA = wandering albatross, WCP = white-chinned petrel

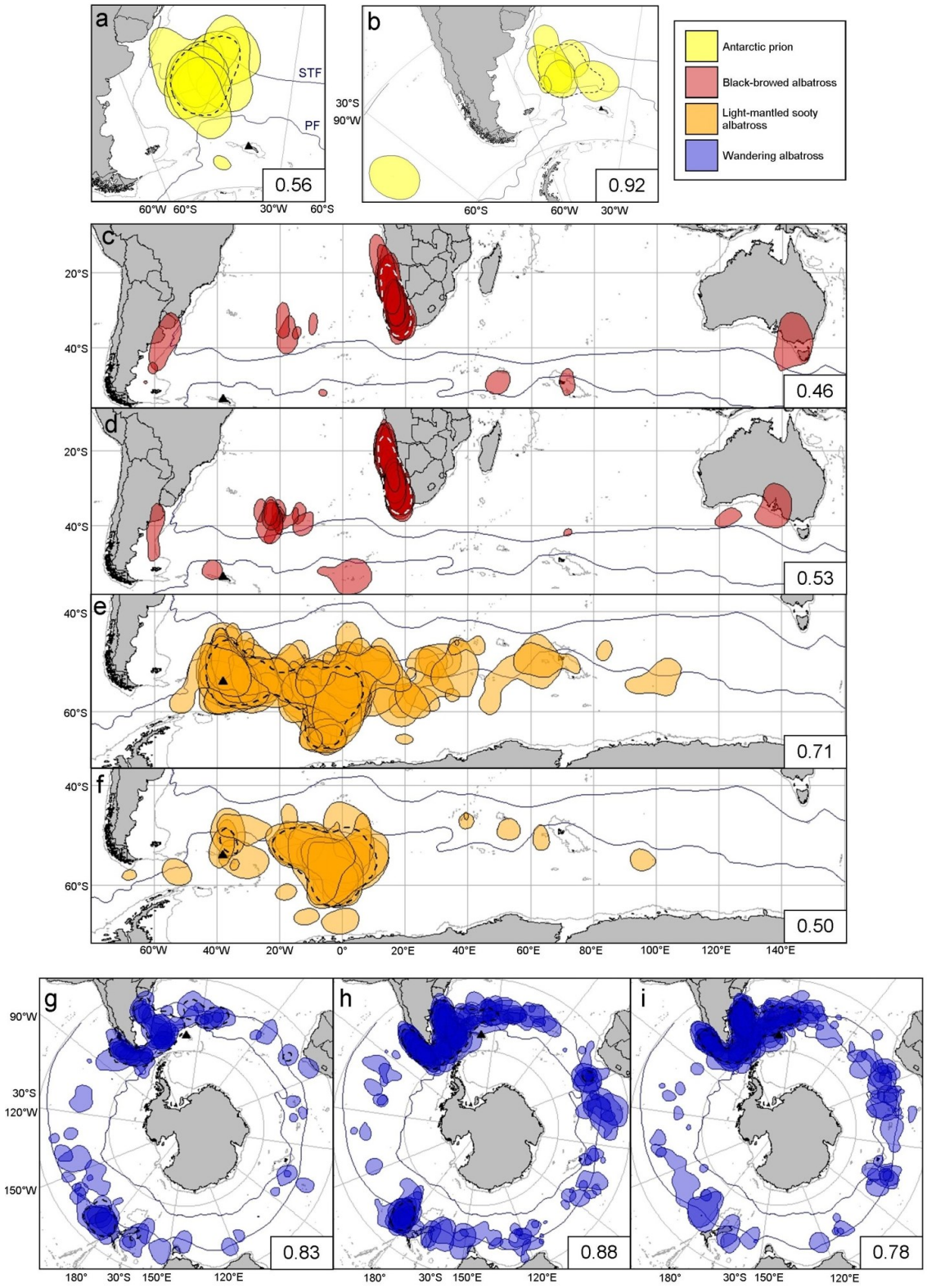


Figure 2.3. Map of core (50% UDs) areas of individuals, shown by overlaying coloured polygons, for four species tracked in multiple years: a) Antarctic prions (AP) in 2010, b) Antarctic prions in 2011, c) black-browed albatrosses (BBA) in 2002, and d) in 2003, e) light-mantled sooty albatrosses (LMSA) in 2004, and f) in 2005, g) wandering albatrosses (WA) in 2004, h) in 2008, and i) in 2009. The core area (50% UD) of the population is shown by a hashed white or black line, where appropriate. For each species-year, an index of individual variability between 0 and 1 (where 0 = all individuals overlap completely, and 1 = all individuals are segregated spatially), is shown in the bottom-right box. Bird Island is displayed as a black triangle and the annual position of the Subtropical (STF) and Polar Fronts (PF) are shown as dark blue lines and the 1,000 m isobath as a grey line. Brown skuas not included as both individual and population kernels are provided in Carneiro et al. (2016)

Individual variability was the main driver of minimum sample sizes, and explained a large amount of variance (Fig. 2.4, Table A1.3 in Appendix 1). The size of the core area of the population was also important, such that species with larger core areas (GHA and WA) required larger minimum samples (Table 2.2, Fig. 2.1). Surprisingly, the predicted minimum sample size was not influenced by the original sample size (Table A1.3 in Appendix S1.2). The extent of individual variability varied among species (Fig 2.4); for core areas, the values ranged from 0.43 for SGP to 0.98 for BS in 2012, and for general use areas from 0.27 for NGP to 0.63 for BS in 2012. Individual variability was similar between years for some species (BBA and WA), but not others (AP, BS and LMSA) (Fig. 2.4).

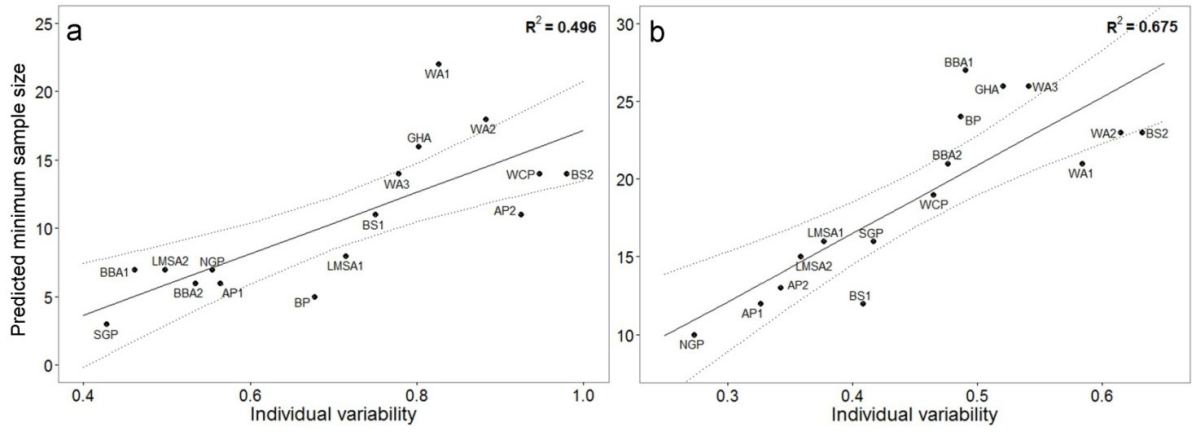


Figure 2.4. The relationship between individual variability, an index between 0 and 1 (where 0 = all individuals overlap completely and 1 = all individuals are segregated spatially), and the predicted minimum sample size for a) core (50% UD), and b) general use (95% UD) areas of 10 species of seabirds tracked with geolocators from Bird Island, South Georgia. The modelled line is derived from GLMM containing just the fixed effect of individual variability and is shown with 95% confidence intervals as dotted lines. The marginal R^2 of the model is displayed in the top-right corner. AP = Antarctic prion, BBA = black-browed albatross, BP = blue petrel, BS = brown skua, GHA = grey-headed albatross, LMSA = light-mantled sooty albatross, NGP = northern giant petrel, SGP = southern giant petrel, WA = wandering albatross, WCP = white-chinned petrel.

2.4 Discussion

2.4.1 How many individuals are required to represent home ranges?

Previous studies have concluded that large numbers of individuals (>30) are required to represent population home ranges (Hebblewhite and Haydon, 2010; Schofield et al., 2013), yet such recommendations are seldom quantitative. Contrary to the assumption that large numbers of individuals would need to be tracked for wide-ranging species (Soanes et al., 2013; Gutowsky et al., 2015), I find that the minimum number required to represent core and general use areas of seabirds during the non-breeding season is relatively modest (Table 2.2). Indeed, predictions were substantially lower than those for breeding seabirds tracked with GPS devices that forage predominantly in coastal or continental shelf waters (Soanes et al., 2013; Warwick-Evans et al., 2016). This difference partly relates to the spatial scale of my analysis, with greater smoothing of geolocator data resulting in greater overlap between individuals.

My analysis revealed large variation in minimum sample sizes between species, which was driven by variability among individuals, rather than broad habitat preferences (oceanic or continental shelf) or the original number of birds tracked. Indeed, individual variability alone explained almost 50% and 70% of variance in predicted minimum sample sizes for core and general use areas, respectively. Fewer individuals were required to represent core than general use areas (as in Gutowsky et al., 2015), likely due to the tendency for individuals to aggregate in areas of high prey availability. This study features species with a diverse range

of movement strategies and so our results have broad applications to many migratory species (Bunnefeld et al. 2011, de Grissac et al. 2016). For example, southern giant petrels are largely sedentary around the colony region (González-Solís et al. 2008) and there was little variation between individuals so the minimum sample size predicted was very low. While black-browed albatrosses covered a much larger area, most individuals migrated to a relatively small region of the Benguela Upwelling (Phillips et al. 2008) and so few individuals are required to describe their home range area. White-chinned petrels also migrated to productive shelf-areas but individuals selected usually one of several distinct regions within their range (Humboldt Upwelling, Patagonian Shelf, or Brazil-Falklands Confluence; Phillips et al. 2006) and so a larger number of individuals is required to cover their range. Finally, species such as grey-headed and wandering albatross had a more dispersive strategy, usually consisting of a combination of multiple non-breeding regions and distinct movement strategies that linked them, including one or more circumpolar trip (Weimerskirch and Wilson 2000; Croxall et al. 2005; Weimerskirch et al. 2015; Clay et al. 2016; Chapter 3; 6); and so up to 20-30 individuals were required to encompass population-level patterns. For migratory species with large among-individual variation in movements, such as the Atlantic puffin *Fratercula arctica* (Guilford et al. 2011, Fayet et al. 2016) or leatherback turtle *Dermochelys coriacea* (Hays et al. 2004), a large number of individuals (around the upper end of our predictions) may be required. In contrast, for species where all individuals migrate to the same non-breeding region, such as Murphy's petrel *Pterodroma ultima* (Chapter 4) or white shark *Carcharodon carcharias* (Jorgensen et al. 2010), a sample of 10 individuals may suffice. While my methodology provides a means of predicting the size of the home range of a population even if the existing tracking data are somewhat limited, it does rely on the assumption that movement strategies of the population are represented by the tracked individuals, particularly for species with low sample sizes (Schofield et al., 2013). I therefore advocate caution in drawing inferences from small samples (<10 individuals), as minority migration strategies may be missed (e.g. AP in 2011).

2.4.2 Do minimum sample sizes vary between years?

Although several studies have investigated annual variability in the distributions of seabirds (Kappes et al., 2010; Bogdanova et al., 2014; Yamamoto et al., 2014; Carneiro et al., 2016), few have considered whether the minimum number of individuals necessary to represent the home range of the population varies annually. In this study, core distributions of most

populations tracked over more than one non-breeding season were similar between years (Fig. 2.3), yet there was variability in requisite sample sizes. As my samples were not balanced between years, I sub-sampled to determine whether differences in predicted minimum sample sizes were due to the size of the sample or the variability among individuals. For species where the majority of individuals used similar core areas in multiple years (AP and LMSA), the lower sample size in one year had a limited influence on the minimum sample size predicted. This was not always the case, however, as sub-sampling the larger BS sample resulted in lower minimum sample size predictions, suggesting that sample size was the main driver (Carneiro et al., 2016). For species with greater individual variability in distributions (WA and BBA), the chance selection of individuals within the sample appeared to drive annual differences in predictions. For example, predicted sample sizes were lower for WA in 2009 because fewer individuals visited the New Zealand region. This emphasises the challenge, particularly with limited sample sizes, of differentiating between individual variability and annual effects (Gutowsky et al., 2015).

I did not consider annual variability in relation to environmental influences, yet many seabirds adjust their foraging behaviour to track changes in oceanographic conditions (Kappes et al., 2010; Yamamoto et al., 2014; Warwick-Evans et al., 2016). Despite this, one or two years of tracking of an inshore species, the European shag *Phalacrocorax aristotelis*, captured the majority of the core used by a population over 15 consecutive years (Bogdanova et al., 2014). The studies that have examined annual differences in non-breeding distributions and habitat preferences suggest that many species consistently use the same areas (Yamamoto et al., 2014), especially if these are characterised by static oceanographic features (Carneiro et al., 2016). This suggests that the common practice of pooling data in order to compare species tracked in different years (Delord et al., 2014; Raymond et al., 2014; Lascelles et al., 2016), may suffice for identifying predictably important habitats for marine predators.

2.4.3 Implications for conservation

Tracking data are used increasingly to identify key habitats for marine predators (e.g. important bird areas or IBAs; Delord et al., 2014; Lascelles et al., 2016). These could be incorporated into networks of MPAs (Ronconi et al., 2012) or used to better understand potential overlap with fisheries (Jiménez et al., 2016), and areas of oil and gas exploration (McFarlane Tranquilla et al., 2013). Despite the obvious potential, only a minority of tracking

studies seem to directly inform conservation management (Jeffers and Godley, 2016), and there are suggestions that limited funds may be better spent on direct action rather than further tracking (McGowan et al., 2016). Also, there is evidence that carrying devices for extended periods of time may have negative effects on animal well-being, especially for smaller species (reviewed in Burger and Shaffer, 2008). Although large-scale collaborative data-sharing projects are enabling researchers to gain a synoptic view of multi-site and multi-species patterns (Coyne and Godley, 2005; Ramos et al., 2013; Lascelles et al., 2016), they do not guarantee population-level inference (Hays et al., 2016), particularly as animals from different populations can have distinct movement strategies and habitat preferences (Clay et al., 2016, Chapter 3).

The principal aim of this study was not to define important at-sea areas for non-breeding seabirds from South Georgia, however I emphasize that the identification of protected areas for pelagic species with substantial individual variability and broad habitat preferences will be particularly challenging (also see Delord et al., 2014). Regardless, this study reveals that the sample sizes required for non-breeding seabirds tracked with geolocators are within the range achieved in some recent studies (<30 individuals). If these recommendations are followed, inferences about important areas used during the non-breeding season should be reliable even for wide-ranging species, and can directly inform their conservation and management.

2.5 Abstract

Individual-based tracking data from marine predators are used increasingly to identify biodiversity hotspots and priority areas for conservation, particularly in the open ocean. Although the issue of sample size is integral to good experimental design and population-level inference, little attention has been paid to how many individuals are required to represent the home range of a population, particularly outside the breeding season. Using an unusually comprehensive dataset for 10 species of pelagic seabirds tracked with geolocators over 305 individual non-breeding seasons, I determine the minimum number of individuals required to predict important areas for populations, accounting for individual and annual variability in spatial distributions. I investigated the relationship between sample size and home range area using a resampling approach and quantitatively assessed the minimum sample size required. The number of individuals needed to adequately represent core (50% utilization distribution, UD) and general use areas (95% UD) of a population, were relatively modest, ranging from 3 to 22 and 10 to 27, respectively, depending on the species. Variability among individuals was the main driver of between-species and between-year differences in predicted minimum sample sizes, and inferences from low sample sizes (< 10 individuals) should be viewed with caution, particularly for species with variable migration strategies. The identification of important areas for migratory animals requires a better understanding of population-level movements and habitat utilization. My recommendations of minimum sample sizes should make researchers and conservation practitioners aware of the potential limitations of some datasets, and can assist in the planning of targeted tracking studies or when making inferences from existing tracking data. I provide advice to ensure that sample sizes are sufficient for informing marine spatial planning, and highlight the potential pitfalls when using tracking data to identify key sites or potential marine protected areas for seabird populations

3 PROXIMATE DRIVERS OF SPATIAL SEGREGATION IN NON-BREEDING ALBATROSSES

This Chapter is also published in Clay T.A., Manica A., Ryan P.G., Silk J.R.D., Croxall J.P, Ireland L., & Phillips R.A. (2016) Proximate drivers of spatial segregation in non-breeding albatrosses. *Scientific Reports*, **29932**.

3.1 Introduction

Partitioning of resources between ecologically-similar animals promotes their coexistence, and often involves the use of different areas or habitats (Lack, 1971; Schoener, 1974). To avoid competition, animals may exploit the same geographic space by having non-overlapping ecological niches, reflecting differences in diet, habitat or foraging behaviour (Croxall and Prince, 1980; Navarro et al., 2013; Wakefield et al., 2013). Alternatively, conspecifics often segregate in geographic space, although sometimes exploit a similar habitat; however, habitat specialization may arise from the use of mutually-exclusive areas separated by distinct habitat boundaries (Wakefield et al., 2011; Thiebot et al., 2012).

Colonial species such as seabirds frequently target seasonally productive areas, which can lead to intense competition among breeding birds constrained to return to land to incubate eggs or feed dependent young. Thus, seabirds are useful tools for studying the relationship between extrinsic factors such as resource availability and competition as well as intrinsic habitat preferences (Matthiopoulos, 2003; Wakefield et al., 2011). Birds must respond to

seasonal changes in prey availability, yet they also experience differing levels of competition as breeding constraints change (Wakefield et al., 2011). Additionally, factors such as body size or wing loading, energy or nutrient requirements, are important drivers of segregation (Shaffer et al., 2001b; Phillips et al., 2004a).

Outside the breeding period, seabirds have fewer constraints and disperse over wider areas (e.g. Croxall et al., 2005), and so their foraging niche may be a better representation of intrinsic preferences. The recent development of miniaturized tracking devices has revealed amongst the longest known migrations on Earth, including trans-equatorial or circumpolar trips (Croxall et al., 2005; Shaffer et al., 2006; Egevang et al., 2010). This vagility suggests few physical barriers to dispersal, yet recent evidence suggests that segregation during the non-breeding season may be a key determinant of population genetic structure (Friesen et al., 2007; Rayner et al., 2011). In species with high movement costs such as penguins, competition and niche partitioning often leads to spatial segregation (Thiebot et al., 2012; Ratcliffe et al., 2014); however, in more mobile species such as trans-equatorial shearwaters, there can be substantial mixing of distinct populations (Shaffer et al., 2006; Catry et al., 2011a). In addition, the few studies that investigate within-population differences indicate that non-breeding birds of different sex and breeding outcome vary in their space or habitat use, with implications for population structure and dynamics (Phillips et al., 2009a; Bogdanova et al., 2011).

Grey-headed albatrosses *Thalassarche chrysostoma* (hereafter GHA) forage in highly seasonal environments and often associate with frontal systems between Antarctic and sub-Antarctic waters (Scales et al., 2016). In a pioneering tracking study, GHA from South Georgia exhibited a diversity of migration strategies; some remained resident in the southwest Atlantic, whereas others travelled to the southwest Indian Ocean, or undertook one or more circumpolar trips during a single non-breeding period (Croxall et al., 2005). As such, they are an excellent model species for investigating large-scale space use of animals over time. GHA breed every two years, with a non-breeding duration of around 16 months, so deferring breeders represent a substantial proportion of the population (Croxall et al., 2005; Ryan et al., 2007). There are major populations at seven island groups, and c. 50% of global numbers are at South Georgia (Poncet et al., 2006) (Appendix Table A2.1). The non-breeding distributions of other populations are so far unknown, as are the movements of failed birds.

In this study I modelled the distributions of non-breeding GHA from different populations within a use-availability framework (Matthiopoulos, 2003). I compare the spatial predictions of various hypothesized drivers of space use to determine which best explained the observed patterns. This study investigates 1) the degree of spatial segregation among and within populations, 2) the influence of extrinsic factors (habitat availability and intra-specific competition) on distributions, and 3) the influence of intrinsic factors (population, sex, breeding outcome and individual) on the habitat preferences and distributions of albatrosses.

3.2 Methods

3.2.1 Logger deployment and processing

Fieldwork was carried out on two widely-separated populations; Bird Island, South Georgia (hereafter SG) in the southwest Atlantic Ocean (54°00' S, 38°03' W) and Marion Island, Prince Edward Islands (hereafter PEI) in the southwest Indian Ocean (46°54' S, 37°45' E). Together these archipelagos represent >60% of the global annual breeding population (Table A2.1). Previously successful breeders were tracked from both SG (n = 22) and PEI (n = 24), and failed breeders from SG (n = 19) (see Appendix 2 for details). Handling time for deployment and retrieval of tracking devices was <10 minutes. GHA are sexually size-dimorphic (Phillips et al., 2004a), and most birds were sexed from bill measurements.

Light data were processed in MultiTrace, providing two positions per day with a mean error of 186 km ± 114 km (Phillips et al., 2004b). I excluded locations with interruptions around sunrise and sunset, and periods around the equinox (2 to 4 weeks), when latitude cannot be estimated reliably; however, individual departure and arrival times could still be derived from longitudinal movements. I created utilization distribution (UD) kernels to show spatial patterns, with the 50% and 90% UDs representing core and general use areas. To control for individual differences in tracking durations, UDs were generated for each bird and then merged so there was equal representation in the larger sample. I selected a grid size of 50 km and smoothing parameter of 200 km to account for tag error (Phillips et al., 2004b, 2005).

Distributions of birds were compared in summer (mid-September to mid-May, coinciding with the breeding season) and winter (mid-May to mid-September). To determine if samples were sufficient to represent each population, a bootstrapping approach was used to randomly

sample home-range area with an increasing number of individuals (Hindell et al., 2003) (see Appendices 1 and 2 for details).

3.2.2 Spatial segregation

To test whether albatrosses segregate by population, sex, breeding outcome and season, I calculated the overlap between home ranges using the utilization distribution overlap index (UDOI), which is considered the most appropriate measure of overlapping space use (Fieberg and Kochanny, 2005). I used a randomization procedure to determine if observed spatial segregation was greater than expected by chance; *P*-values were determined as the proportion of randomized overlaps that were smaller than the observed (Breed et al., 2006). In order to make sure results were repeatable across overlap indices, I compared results using the UDOI method with that of the home-range method (PHR) which measures the proportion of overlap of home-ranges at certain isopleths, in this case the 50% and 90% isopleths (Fieberg and Kochanny, 2005) (see Appendix 2 for details). For ease of interpretation, only results from the UDOI method are reported in the main text (see Table A2.2 for PHR results).

3.2.3 Habitat modelling

I used a habitat preference modelling approach to quantify space use as a function of available habitat, by comparing where an animal was observed (tracking location) with where it could have gone (pseudo-absence), if it had no particular preference (Aarts et al., 2008). I simulated tracks, accounting for availability of suitable habitat by incorporating individual movement constraints, which is particularly important for GHA given the large variability in migration strategies (Croxall et al., 2005). Simulations for each individual were correlated random walks (CRW) generated in the R package adehabitatLT (Calenge, 2006) using two movement parameters: step length and turning angle. I tested the effects of different numbers of simulations on model performance (Žydelis et al., 2011) (see Appendix 2 for details).

As animals rarely respond to the environment in a linear way (Aarts et al., 2008), I used a generalized additive modelling (GAM) approach with smooth splines for environmental predictors and a binomial error structure (Wood, 2006). I selected static and dynamic variables known to be important for albatrosses (Nel et al., 2001; Catry et al., 2004; Scales et al., 2016) (Table A2.3), including 1) sea surface temperature (*SST*) and 2) gradient as measured by the standard deviation of *SST* (*SST std*), indicative of water mass and frontal

regions; 3) chlorophyll α concentration (*Chl*) as a proxy of ocean productivity; 4) ocean floor depth (*Depth*) and 5) slope, represented by the standard deviation of *Depth* (*Depth std*), to indicate productive bathymetric areas such as shelf-breaks, seamounts and upwelling; 6) sea-level anomaly (*SLA*) and 7) eddy kinetic energy (*EKE*) as indicators of mesoscale oceanography associated with currents and eddies; and 8) wind speed (*Wind*) as albatrosses are known to be constrained by high flight costs (Wakefield et al., 2009b). I also incorporated; 9) minimum distance to the colony (*Dist. own*) and 10) minimum distance to the closest other colony (*Dist. closest*) to determine the importance of habitat accessibility and intra-specific competition, which limit distributions of breeding albatrosses (Wakefield et al., 2011). Oceanographic variables were sampled within a temporal window of each location in observed and simulated tracks (see Appendix 2 for details).

I constructed separate models for different classes of birds because of computational demands and difficulties of interpreting high order interactions. Initial models testing for interactions between population and season were significant, so I split the model into four components, by population (SG vs. PEI) and season (summer vs. winter). For each model, I ran all possible combinations of predictors and calculated AIC values using the dredge function in the R package MuMIn (Bartoń, 2015). Candidate models were ranked according to AIC and weight. I then individually assessed the importance of variables based on proportion of deviance explained (see Appendix 2 for details). For PEI models I included the tracking year as a fixed effect to test for annual differences in distributions, then compared models with and without year and selected those with the lowest AIC values.

To identify the main extrinsic drivers, I constructed models representing habitat (habitat variables), the constraints associated with competition and accessibility (distance variables), and the full model (all variables). I used area under the receiver operator characteristic (ROC) curve (AUC) to evaluate performance of models on a weekly basis, in the PresenceAbsence package in R (Freeman, 2012). Values of 0.5-0.7, 0.7-0.9, and >0.9 represent poor, reasonable and very good model performance, respectively. I created spatial predictions for each population in summer and winter using the cut-off of highest sensitivity and lowest proportion of false positives along the ROC curve to distinguish suitable and unsuitable habitat. I compared weekly AUC scores of the three predictor types to determine which drivers (full, habitat or distance constraints) best matched observed spatial patterns (see Appendix 2). I also tested transferability of population-specific models across sites by cross-

validation using AUC scores, whereby each individual was a data fold. Iteratively, each model was trained on all-but-one fold and tested on the remaining one, withholding each fold in turn. Metrics of model performance thus took individual differences into account.

To test for intrinsic influences of sex and breeding outcome (failed or successful) on space use, I ran models with and without these variables as smoothers. To assess sex differences, I used the original four population models (above), and to assess breeding outcome differences, I used the pooled dataset of failed and successful birds from South Georgia during summer and winter. I tested model performance on each individual, as above, comparing the resulting AUC scores of models with and without sex- and breeding outcome-specific smoothers. All analyses were conducted in the software R v. 3.1.1 (R Core Team, 2014). Unless otherwise indicated, values are presented as mean ± SD.

3.3 Results

The non-breeding migrations of 66 grey-headed albatrosses were tracked from SG and PEI, comprising 46 previously successful and 20 failed birds. The successful breeders were tracked for 490 ± 78 days (range 92 – 815), covering the whole non-breeding period (winter-summer-winter) for all but three birds with logger batteries that failed before retrieval. For both SG and PEI, bootstrapping analyses confirmed that sample sizes were sufficient to make population-level inferences (Fig. A2.1). Nineteen breeders that had all failed during incubation in late December - early January (mean 25 December ± 20 d) were tracked from SG for the subsequent 277 ± 21 days (range 242 – 334). As only one failed bird from PEI was tracked, this individual was excluded from analyses. Consequently, among-population comparisons were conducted on successful individuals, and comparisons between successful and failed breeders were made on SG birds only.

3.3.1 Patterns of spatial segregation

3.3.1.1 Among-population differences

Birds from both populations exhibited a diverse suite of migration strategies encompassing a range of oceanic habitats within the Southern Ocean (see Appendix 2 for details). Despite this high vagility, the two distributions were more spatially segregated than expected (observed overlap 0.55 and randomized overlap 1.53 ± 0.09, $P < 0.001$; Table 3.1), as different ocean

sectors were used at different times (Fig. A2.3). Successful birds from SG (n = 22) spent a large proportion of time in the southwest Atlantic; north of the colony between the Polar Front and the Subtropical Front, east of the Falkland Islands, and around the South Sandwich Fracture Zone (Fig. 3.1b). They also foraged around the Subtropical Front in the southwest Indian Ocean and northeast of the Kerguelen Plateau towards the Southeast Indian Ridge. In contrast, birds from PEI (n = 24) spent a large proportion of time in the Indian Ocean; around the colony towards the Southwest Indian Ridge and in the southeast Indian Ocean between the Kerguelen Plateau and Southeast Indian Ridge (Fig. 3.1c). They also foraged towards the Humboldt Upwelling, southeast Pacific Ocean. Spatial segregation persisted during the non-breeding summer and during both winters, but was greater in summer (observed overlap 0.40 and randomized overlap 1.35 ± 0.10, $P < 0.001$; Table 3.1) than winter (observed overlap 0.61 and randomized overlap 1.97 ± 0.16, $P < 0.001$; Table 3.1, Fig. A2.2). The distribution of PEI birds tracked in 2002 and 2003 was broadly similar (observed overlap 2.16; randomized overlap 2.12 ± 0.18, $P = 0.58$), although birds in 2002 were more likely to use the southeast Pacific (Fig. A2.4).

3.3.1.2 Within-population differences

There was no evidence of sexual segregation across the whole utilization distributions (pooled dataset UDOI method; observed overlap 1.47 and randomized overlap 1.60 ± 0.20, $P = 0.070$; Table 3.1); however, I did find males and females from SG segregated in their core (50%) but not general use (90%) distributions during summer only (Table A2.2, Fig. A2.5). Females from both populations also used higher latitudes than males by c. 1°, year-round (GLMM: $X^2_1 = 6.0$, $P = 0.014$; Table 3.2). Males in both populations departed 6 days later than females (GLMM: $X^2_1 = 5.1$, $P = 0.024$), but did not differ in return dates (GLMM: $X^2_1 = 2.0$, $P = 0.15$). There was no evidence that males from either population travelled further than females, or varied more in their migration characteristics (Table 3.2).

Table 3.1. Observed and randomized overlap (utilization distribution overlap index, UDOI) of utilization distributions (UD) between different groups of grey-headed albatrosses; population (South Georgia or SG and Prince Edward Islands or PEI) by season, sex by population and season, and breeding outcome by season.

Class		Observed	Randomized	*P*
Population (All successful)				
	Summer	0.40	1.35 ± 0.10	**<0.001**
	Winter	0.61	1.97 ± 0.16	**<0.001**
Sex (All successful)				
	PEI Summer	1.49	1.52 ± 0.16	0.35
	PEI Winter	2.18	2.58 ± 0.29	0.074
	SG Summer	1.33	1.32 ± 0.24	0.50
	SG Winter	1.31	1.16 ± 0.28	0.72
Breeding outcome (All SG)				
	SG Summer	1.01	1.45 ± 0.17	**0.001**
	SG Winter	1.71	1.65 ± 0.20	0.61

Breeding outcome comparisons are for SG only. Randomized overlaps are shown as a mean ± SD and P represents the proportion of randomized overlaps that were smaller than the observed. For more information see Appendix 2. Significant differences are shown in bold.

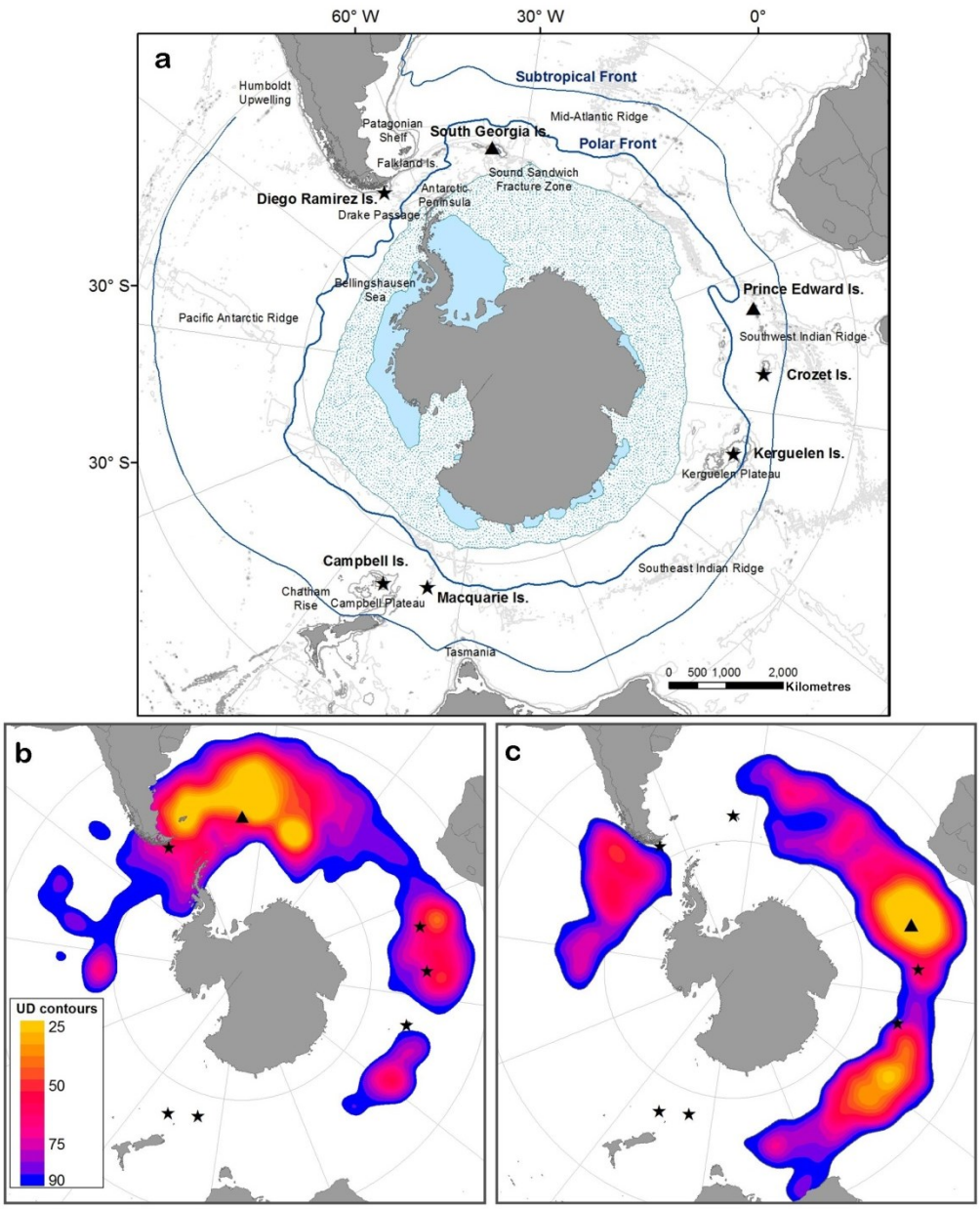


Figure 3.1. a) Map of the study region including the minimum summer (light blue) and maximum winter (dotted blue) sea ice extents (>15% concentration), and 500m, 1000m and 3000m isobaths. The non-breeding utilization distributions (UDs) of successful grey-headed albatrosses *Thalassarche chrysostoma* from b) Bird Island, South Georgia, and c) Marion Island, Prince Edward Islands. UD contours are shown in 5% intervals ranging from 25% (yellow) to 90% (dark blue). Black triangles and black stars indicate study colonies, and other breeding populations, respectively.

Table 3.2. Comparison of migration characteristics (mean ± SD) of grey-headed albatrosses from Bird Island, South Georgia (SG) and Marion Island, Prince Edward Islands (PEI) by population and by sex.

	Population				Sex			
	P	X^2	SG	PEI	*P*	X^2	Female	Male
Departure date	0.17	1.9	9 May (±10)	6 May (±9)	**0.024**	5.1	5 May (±10)	11 May (±7)
Return date	**0.002**	9.9	23 Sept. (±6)	3 Sept. (±6)	0.15	2.0	16 Sept. (±12)	9 Sept. (±10)
Non-breeding period (days)	**0.003**	8.6	502 (±12)	486 (±10)	**0.005**	7.9	499 (±13)	487 (±10)
Proportion circumpolar (%)	0.06	3.5	52 (±51)	83 (±38)	0.89	<0.1	67 (±48)	72 (±46)
Cumulative distance (km)	0.27	1.2	161,000 (±26,000)	173,000 (±21,000)	0.87	<0.1	166,000 (±27,000)	168,000 (±20,000)
Mean distance/day (km)	0.46	0.5	381 (±55)	398 (±44)	0.72	0.1	386 (±54)	397 (±44)
Maximum range (km)	**0.037**	4.4	6,700 (±2,900)	8,200 (±1,200)	0.86	<0.1	7,400 (±2,500)	7,600 (±1,900)
Mean longitude (°)	**<0.001**	11.3	-19.1 (±21.9)	33.7 (±20.2)	0.29	1.1	1.8 (±35.3)	20.0 (±28.9)
Mean latitude (°)	**0.019**	5.5	-48.5 (±1.6)	-47.1 (±1.6)	**0.014**	6.0	-47.4 (±1.7)	-48.2 (±1.8)
Area 50% UD (10^6 km^2)*	0.77	0.1	2.9 (±1.1)	2.9 (±1.1)	**0.028**	4.8	3.2 (±1.2)	2.5 (±0.8)
Area 90% UD (10^6 km^2)*	0.37	0.8	14.0 (±7.1)	15.1 (±5.0)	0.28	1.2	15.3 (±6.5)	13.4 (±5.2)

P-values are the result of GLMMs of population and sex. Observed means are given and have been calculated from the pooled dataset. For more information see Appendix 2. Proportion circumpolar represents the percentage of birds that performed circumpolar trips. Significant differences are shown in bold.

**Average area of UD for individual birds*

Failed birds from SG dispersed significantly less than successful birds (GLMM: $X^2_1 = 14.9$, $P < 0.001$), probably due to their shorter non-breeding period (8 *vs.* 16 months), as they covered a similar mean distance per day (GLMM: $X^2_1 = 2.7$, $P = 0.11$; see Appendix 2 for details). During summer, failed birds used more southerly areas than successful birds, and consequently, segregation was greater than expected by chance (observed overlap 1.01 and randomized overlap 1.45 ± 0.17, $P = 0.001$; Table 3.1, Fig. 3.2a). During winter, as with successful birds, many failed GHA moved east to forage in the southwest Indian Ocean (Fig. 3.2b); consequently, there was no apparent spatial segregation from successful birds during winter (observed overlap 1.71 and randomized overlap 1.65 ± 0.20, $P = 0.65$; Table 3.1). All failed GHA returned to breed the following season, but arrived slightly later (4 days) than previously successful non-breeders (GLMM: $X^2_1 = 5.8$, $P = 0.022$; Table 3.3).

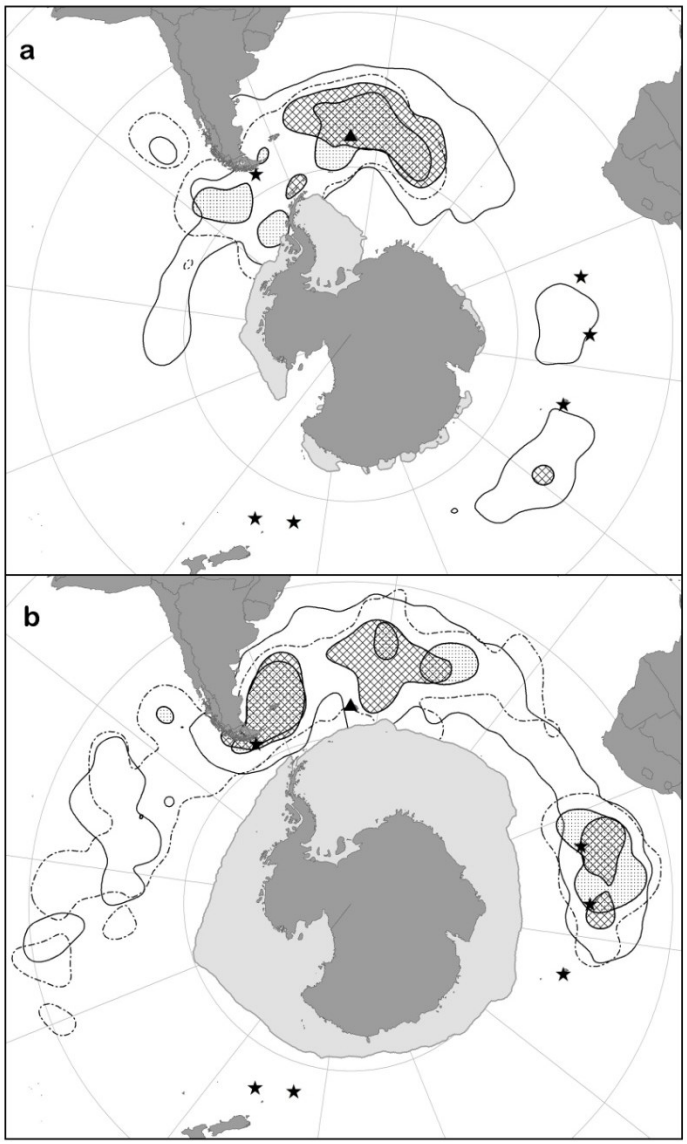


Figure 3.2. The core (50 %) and general (90%) utilization distributions (UDs) of previously successful and failed grey-headed albatrosses from South Georgia, A) in summer, and B) in winter. Core areas are shown for failed and successful birds with hashed and dotted fill, respectively, and for general areas solid and dotted line type, respectively. The minimum summer and maximum winter sea-ice extents (<15% concentration) are shown. Black triangles and black stars indicate the study colonies, and other breeding populations, respectively.

3.3.2 Drivers of spatial segregation

3.3.2.1 Among-population differences

For all four groups, the full model received the most support (>77% weight in each case) (Table A2.7). The inclusion of tracking year improved model fit for birds from PEI during both summer (ΔAIC = -4.14) and winter (ΔAIC = -13.62), but explained a negligible proportion of model deviance (Fig. A2.7). There was a large variation in performance of weekly, and individual-based cross-validation, indicating that observed distributions were predicted much better in some weeks than others, and that population-level models predict the space use of some, but not all individuals (Tables A2.4, A2.5 and A2.6). Furthermore, the predictive performance (AUC) of models cross-validated between sites was always poor; during winter, PEI to SG = 0.57 and SG to PEI = 0.52; and during summer, PEI to SG = 0.52 and SG to PEI = 0.54. Consequently, I made no attempt to predict distributions of birds using models developed for the other population.

Distributions of both populations were best explained by models that included habitat preferences and constraint variables associated with competition and accessibility (see Appendix 2 for details). However, the modelled responses of birds to important predictors differed with season and population. Both distance variables explained longitudinal patterns in albatross movements which were not linked directly to preferences for a particular habitat. Essentially, birds from both populations were more likely to avoid other colonies during summer than winter, and birds from PEI were more likely to avoid other colonies than birds from SG (Fig. 3.3).

Table 3.3. Non-breeding characteristics (mean ± SD) of previously successful and failed grey-headed albatrosses from Bird Island, South Georgia.

			Breeding outcome	
	P	Test	Successful	Failed
Departure date	**<0.001**	1733	9th May (±10)	25th Dec. (±20)
Return date	**0.022**	5.8	23rd Sept. (±6)	27rd Sept. (±7)
Non-breeding period (days)	**<0.001**	1489	502 (±12)	277 (±21)
Proportion circumpolar (%)	**<0.001**	14.9	52 (±51)	5 (±22)
Cumulative distance (km)	**<0.001**	89.7	161,000 (±26,000)	82,000 (±14,000)
Mean distance/day (km)	0.11	2.7	381 (±55)	354 (±41)
Maximum range (km)	0.07	3.5	6,700 (±2,900)	5,300 (±1,600)
Mean longitude (°)	0.06	3.7	-19.1 (±21.9)	-33.3 (±24.6)
Mean latitude (°)	0.26	1.3	-48.5 (±1.6)	-49.9 (±3.5)
Area 50% UD (10^6 km^2)*	**0.019**	6.1	2.9 (±1.1)	2.0 (±0.6)
Area 90% UD (10^6 km^2)*	**0.007**	8.4	14.0 (±7.1)	7.6 (±2.3)

*P-values are from GLMs including breeding outcome, sex and their two-way interaction. The interaction and the effect of sex were not significant in all cases and are not shown. The test statistics depended on the error structure of the model (see Appendix 2). Proportion circumpolar represents the percentage of birds that performed circumpolar trips. Significant differences are shown in bold.*Average area of UD for individual birds*

Birds from both sites used markedly cooler waters during summer than winter; birds from SG preferred lower SST in both seasons (Fig. 3.3). GHA also preferred areas with large deviations in SST, indicative of frontal regions. During summer, preferences of SG birds were associated with the Antarctic Divergence and Polar Frontal regions, along with PEI birds, and during winter, birds from both populations associated with the Subtropical Front. SG birds targeted more productive regions than PEI birds during both seasons. GHA used both a higher and wider range of chlorophyll regimes in summer than winter, and lower EKE; SG birds also used marginally stronger eddies than PEI birds. Finally, PEI birds preferred areas with gently-sloping bathymetry during summer, but steeper slopes during winter.

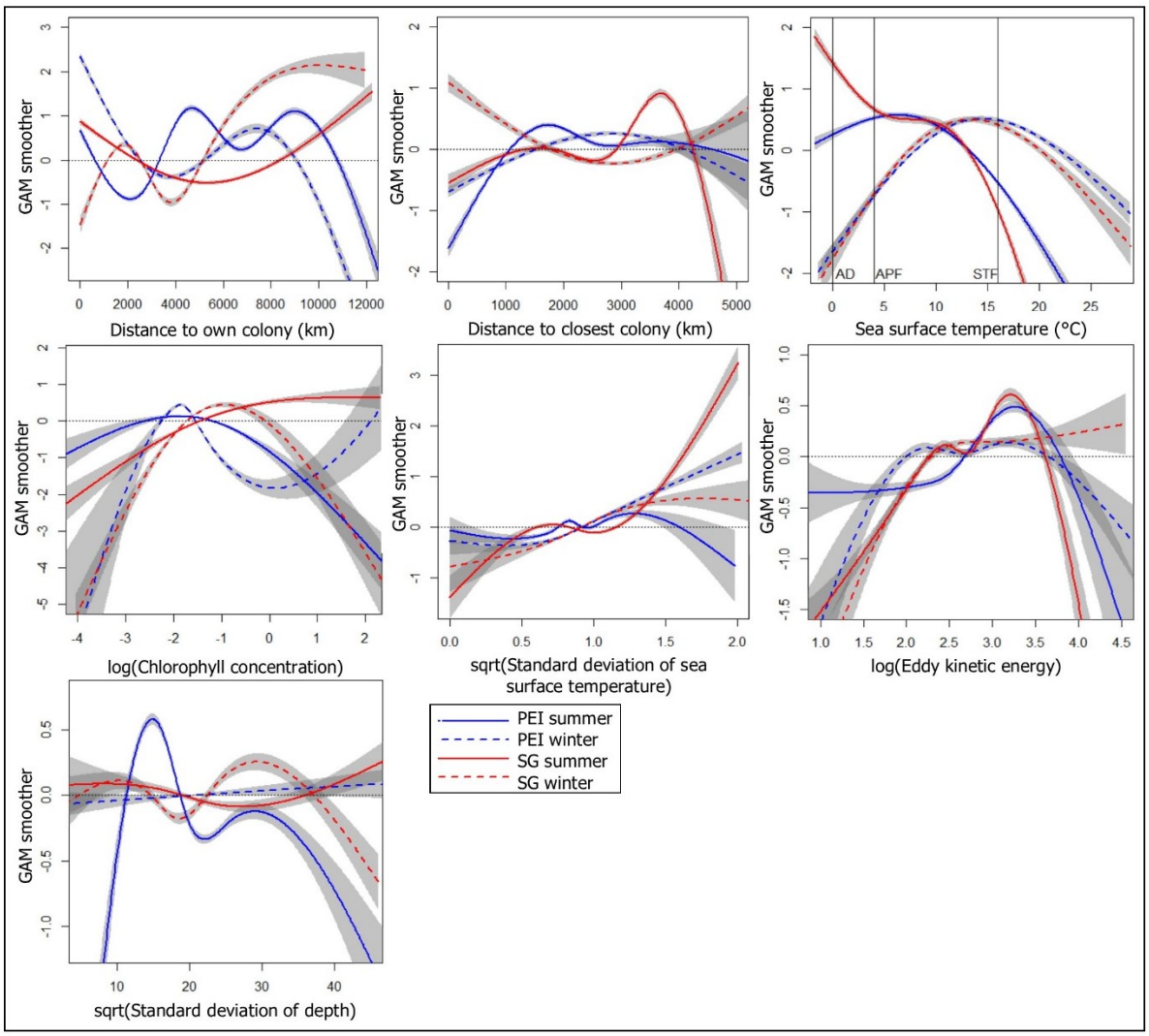


Figure 3.3. Response curves of the most important variables explaining the distribution of previously successful grey-headed albatrosses. Population is represented by colour for South Georgia (SG, in red) and the Prince Edward Islands (PEI, in blue), and season by line type for summer (solid) and winter (dashed). Standard errors of the responses from outputs of generalized additive models (GAM) are shown in grey. Variables were classified as important when they consistently explained more than 1% of model deviance, and are shown in decreasing order of importance from top left to bottom right. Approximate values for major fronts are marked for the Antarctic Divergence (AD), Antarctic Polar Front (APF) and the Subtropical Front (STF). See Appendix 2 for more details.

In slight contrast to the observed distributions, the models including only habitat variables predicted occurrences of GHA over large swathes of the Southern Ocean (Fig. 3.4), indicating that their distributions are limited by competition and accessibility as well as habitat preferences. Moreover, they identified areas of apparently suitable habitat that were not occupied by tracked birds. For example, during winter, both population models predicted high probability of presence east of New Zealand around the Chatham Rise, and on the Campbell Plateau, and the model for PEI predicted that those birds would use the Scotia Sea and waters around the Falkland Islands though birds were not found in these areas.

3.3.2.2 Within-population differences

I found no significant differences in model performance scores with the inclusion of sex-specific preferences, providing no evidence of sexual segregation by habitat (Table A2.6). During summer, but not winter, model performance was significantly better with the inclusion of preferences associated with previous breeding outcome (Table A2.5). Similar variables explained the distributions of successful and failed non-breeders. Habitat preferences of birds of different outcome corresponded more closely than those of successful birds from the two populations (Fig. 3.3 and 3.4), yet there were some noticeable differences, particularly during summer. After breeding failure, birds were more likely to use areas further from SG and hence closer to other colonies, particularly around Diego Ramirez (Fig. 3.2), yet there was little difference during winter (Fig. 3.5). In both seasons, failed birds used less productive areas than successful birds. Failed birds targeted slightly colder and deeper waters in summer, and slightly warmer and shallower waters in winter. Failed birds also used frontal regions more during summer; however, they were less likely to use eddy regions than successful birds, particularly during summer.

3.4 Discussion

In this study, I modelled the non-breeding distributions of a highly mobile marine predator as a function of multiple extrinsic (habitat availability and competition) and intrinsic drivers (habitat preferences, population, sex, breeding outcome). I found that patterns of spatial segregation were explained well by season-specific habitat preferences and competition at both meta-population and population scales.

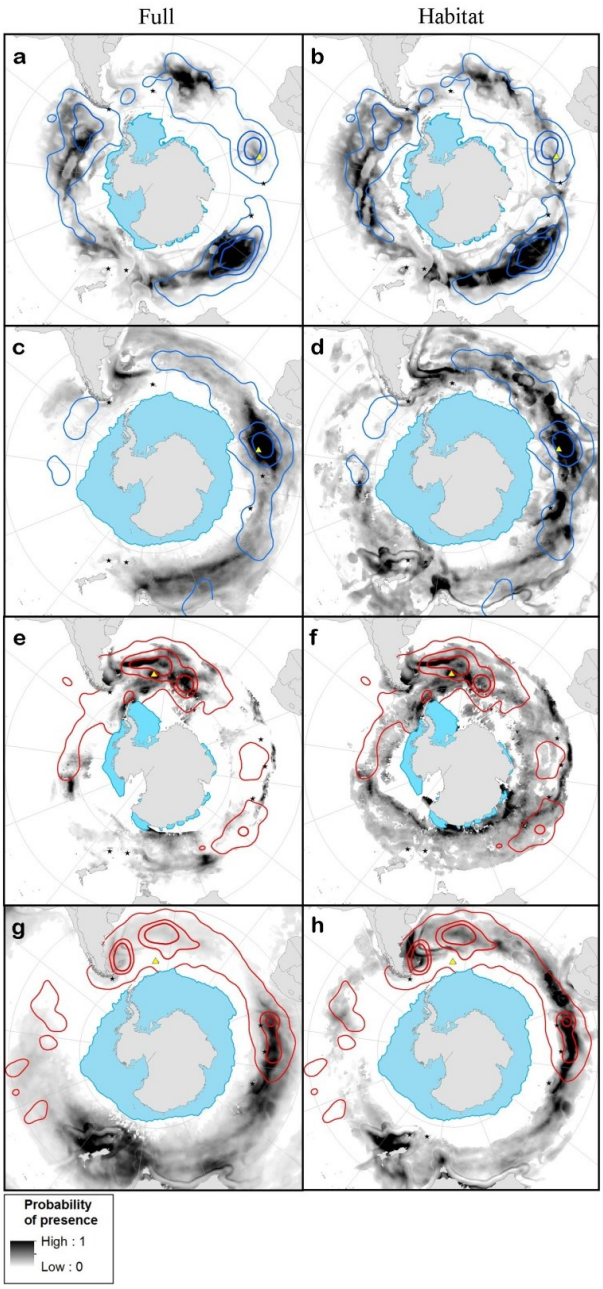


Figure 3.4. Map of the spatial predictions from the full models (left: a, c, e, g), and those just taking into account habitat preferences (right: b, d, f, h). Maps show modelled probability of presence in greyscale of birds from different populations in summer and winter; Prince Edward Islands (PEI) summer (a and b), and winter (c and d), South Georgia (SG) summer (e and f), winter (g and h). The 25%, 50% and 90% kernels of observed distributions are shown for PEI and SG birds in blue and red, respectively. The minimum summer or maximum winter sea ice extents (>15%) are shown as blue polygons and colonies of origin as yellow triangles.

It is challenging to model the distributions of pelagic seabirds as they are highly vagile and often respond to dynamic environmental cues (e.g. Kappes et al., 2010; Žydelis et al., 2011). In particular, the Southern Ocean is a highly seasonal environment with large fluctuations in the positions of major fronts and extent of sea-ice, leading to substantial changes in productivity and prey availability (Smetacek and Nicol, 2005). My seasonal models captured broad temporal patterns, but were unable to track the responses of albatrosses on weekly or monthly scales. Flexibility in habitat preferences of GHA likely reflects their plastic response to seasonally-changing environmental suitability. Past modelling of albatross distributions has generally assumed that animals track their environment in a fixed way (e.g. Kappes et al., 2010; Žydelis et al., 2011); in contrast, these results emphasize that preferences may vary across long non-breeding periods, particularly for biennially-breeding species. Despite this, I found little evidence that birds from PEI tracked in different years change distribution or habitat preferences; hence, I am confident that the large-scale patterns of spatial segregation persist between years.

Whilst there is substantial evidence that spatial segregation reduces competition in breeding seabirds (Croxall and Prince, 1980; Navarro et al., 2013), few studies have concurrently modelled the importance of competition and habitat preferences on non-breeding distributions. Despite their extremely low movement costs, constraint variables associated with accessibility and intra-specific competition were important predictors of GHA distributions, particularly during summer when the density of conspecifics is likely to be much higher around the colony. Typically, birds remained at least 800-1,200 km away from other colonies, which corresponds well with the foraging ranges of breeding GHA (Table A2.1). This avoidance behaviour explains why birds from PEI avoid the SG area during winter, despite similar habitat preferences. In addition, by including constraints associated with local competition, my models accurately predicted the absence of both SG and PEI birds in waters around New Zealand; areas within range of the substantial breeding population on Campbell Island. Although I have not considered inter-specific competition, it is also likely to play a role in structuring albatross distributions (Phillips et al., 2005). Although, for example, congeneric black-browed (BBA) *Thalassarche melanophris* and Campbell albatrosses *T. impavida* are more specialized in targeting shelf-edges than GHA, in areas such as the Patagonian Shelf and New Zealand sub-Antarctic islands, prey depletion around colonies may be enhanced by the presence of these closely-related species (Wakefield et al., 2011).

I incorporated the movement constraints of albatrosses in my null models, yet for all models, *Dist. own* explained the greatest variance. Thus, despite their extreme vagility, albatrosses have preferences for areas around their own colony that are unrelated to habitat. These findings are counterintuitive, suggesting that albatrosses are willing to tolerate birds from their own population rather than exploit distant profitable patches. The costs of migration may therefore be greater than the negative interactions that might arise from local competition, or perhaps in the case of SG birds, the southwest Atlantic is productive enough to support a very large population, year-round (Wakefield et al., 2014). Alternatively, birds may gain reproductive advantages by remaining close to the colony, such as additional breeding opportunities (Ryan et al., 2007).

Whilst niche partitioning can lead to spatial structuring among seabirds (Croxall and Prince, 1980; Navarro et al., 2013; Quillfeldt et al., 2013), few studies have quantified differences in the habitat preferences of conspecifics during migration (Thiebot et al., 2012; Ratcliffe et al., 2014) Although appearing to be a habitat generalist, the greater than expected spatial segregation of GHA populations appeared to be driven predominantly by population-specific habitat preferences. My predictive maps demonstrate the importance of niche segregation, particularly during the non-breeding summer when, for example, PEI birds appeared to avoid the southwest Atlantic mainly due to habitat preferences rather than avoidance of competition (Fig. 3.4). Although these results contrast with a recent study comparing stable isotope ratios of albatrosses from different populations (Cherel et al., 2013), this is probably because comparisons of $\delta^{13}C$ provide limited resolution of spatial overlap, particularly along longitudinal gradients. Segregation of habitat therefore appears to be the main partitioning mechanism in non-breeding albatrosses, which feed opportunistically at the surface and tend to have relatively wide dietary niches (Phillips et al., 2009a; Cherel et al., 2013). This is also supported by the broad similarity between species in diel activity patterns (Mackley et al., 2010).

Non-breeding GHA have season-specific habitat preferences related to dynamic features (frontal regions and eddies), and birds from the two populations exploited different water masses and productivity regimes. During summer, resident SG non-breeders used similar foraging areas to breeding birds (Catry et al., 2004; Phillips et al., 2004a) colder waters around the Antarctic Peninsula, or slightly warmer waters in the Polar Frontal (PF) zone. During winter, there was considerable niche overlap with PEI birds, and predicted

distributions from habitat preference-only models overlapped more than in summer (Fig. 3.4). Both sets of birds associated with mesoscale oceanic features such as eddies. Habitat preferences of birds from PEI were more seasonally consistent, as they used waters of similar productivity throughout the year. During summer, resident birds used similar areas to breeders, reflecting strong associations with sea level anomalies created by the Agulhas Return Current to the north of the colony, and the PF to the south (Nel et al., 2001). As GHA from both populations appeared to use similar features during the breeding season and non-breeding summer, I suggest that divergent non-breeding niches may arise from local adaptation to familiar habitat during breeding (Rayner et al., 2011; Thiebot et al., 2011b). Resulting specializations during the non-breeding period thus have the potential to influence dispersal patterns and ultimately the genetic structuring of seabird populations (Friesen et al., 2007; Rayner et al., 2011).

Within a population, there is growing evidence that processes operating in one season may influence subsequent performance, known as carry-over effects (Harrison et al., 2011) (COEs). The few studies comparing the space use of seabirds of different breeding performance have found links with winter distribution (Bogdanova et al., 2011; Catry et al., 2013). In GHA, breeding outcome was linked to both space use and habitat selection, as birds that fail were more likely than sabbatical non-breeders to use sub-optimal areas (with lower productivity and mesoscale eddy activity) in the latter part of the summer. However, there appeared to be no segregation between the two groups in winter prior to return to the colony.

The reasons why breeding outcome affected habitat use in summer are unclear, but could arise from variation in individual condition over short or long timescales. Failed breeders may have been in better condition due to their reduced parental effort and so may withstand foraging in poorer quality habitats that are closer to other colonies than their own (Fig. 3.5). Alternatively, it could be that birds were less able to compete for prey with breeding birds around SG and were forced to forage nearer the breeding grounds of the major GHA population at Diego Ramirez (Table A2.1). In other species, failed birds migrate further than successful birds but return to the colony at similar times, or travel less far but return sooner (Bogdanova et al., 2011; Catry et al., 2013). Yet, in biennial breeders, failed birds have less time to moult flight feathers between breeding attempts, which may be energetically costly in the following season.

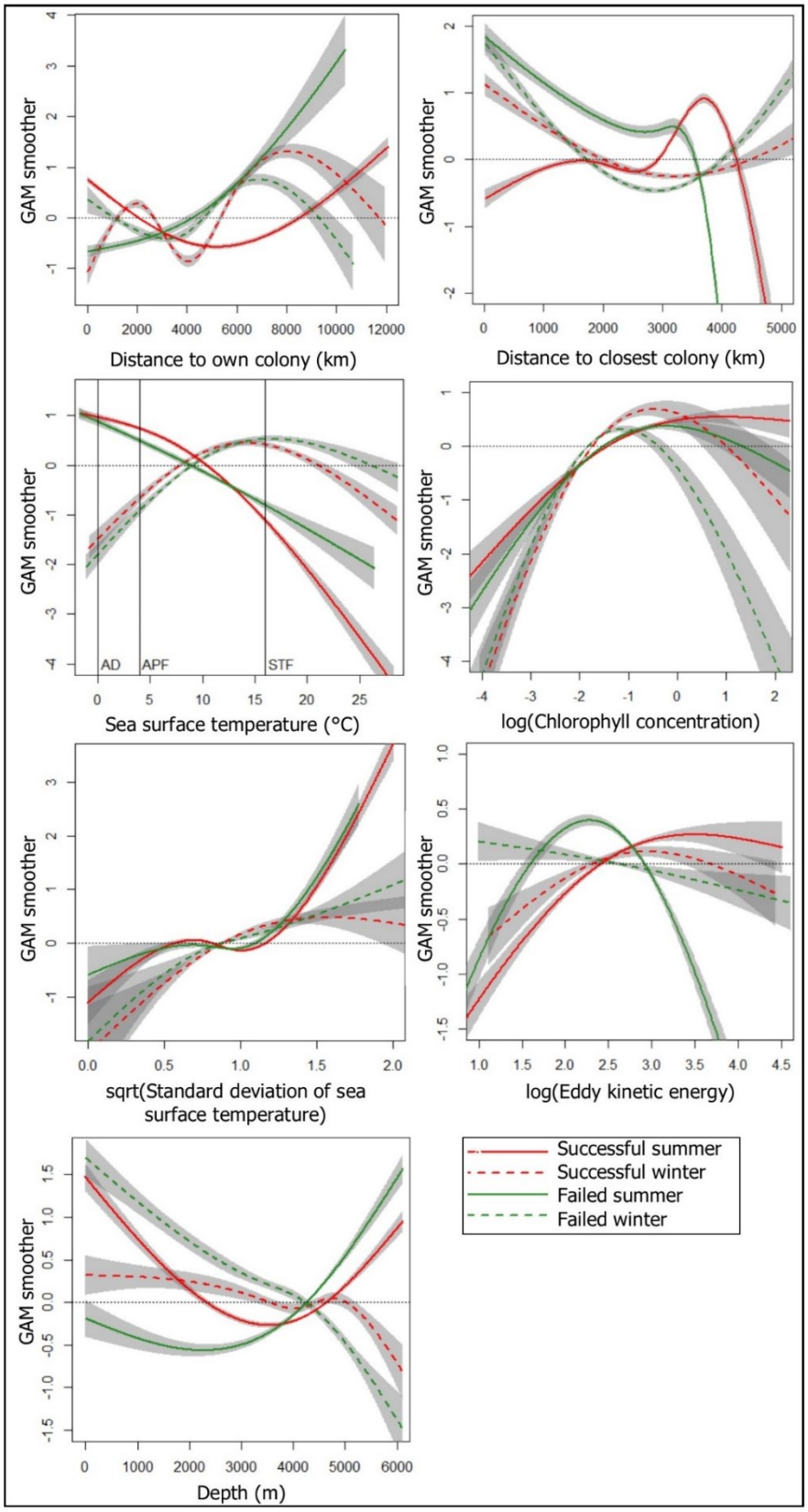

GAM smoother
Distance to own colony (km)
Distance to closest colony (km)
AD
APF
STF
Sea surface temperature (°C)
log(Chlorophyll concentration)
sqrt(Standard deviation of sea surface temperature)
log(Eddy kinetic energy)
Depth (m)
Successful summer
Successful winter
Failed summer
Failed winter

Figure 3.5. Response curves of the most important variables explaining the distribution of previously successful and failed grey-headed albatrosses from South Georgia. Breeding outcome is represented by colour for successful (red) and failed (green) birds, and season by line type for summer (solid) and winter (dashed). Standard errors of the responses from outputs of generalized additive modesl (GAM) are shown in grey. Variables were classified as important when they consistently explained more than 1% of model deviance, and are shown in decreasing order of importance from top left to bottom right. Approximate values for major fronts are marked for the Antarctic Divergence (AD), Antarctic Polar Front (APF) and the Subtropical Front (STF). See Appendix 2 for more details.

In this study the link with subsequent breeding outcome is unknown, yet failed GHA returned to the colony slightly later than successful birds. Late arrival at the breeding grounds can reduce reproductive success in some birds (e.g. Marra et al., 1998), but not others, for example the congeneric BBA (Phillips et al., 2005). Body condition appears to have greater bearing on the breeding decisions of GHA than BBA, and so COEs associated with selection of poorer habitats are likely to be more important (Crossin et al., 2013). Indeed, because GHA breed biennially, they probably have a higher cost of reproduction than annually-breeding *Thalassarche spp*. (Ryan et al., 2007). It is likely that these seasonal interactions reflect other intrinsic factors such as individual quality or breeding experience, and longitudinal studies or experimental manipulations may be necessary to fully disentangle these effects (Catry et al., 2013; Daunt et al., 2014).

In large, dimorphic species such as albatrosses, sex-differences in distributions have been attributed to competition, or the effects of wing-loading on flight performance (Weimerskirch et al., 1993; Shaffer et al., 2001b; Phillips et al., 2004a). In this study, although I found no evidence of sexual segregation in habitat use, females from both colonies foraged at lower latitudes, and the core areas of males from SG were segregated spatially from those of females during the summer. As males do not appear to competitively exclude females from particular habitats, the small degree of sexual segregation seems more likely to be mediated through differences in flight capabilities (Phillips et al., 2004a). My results complement previous findings that $\delta^{13}C$, but not $\delta^{15}N$, is higher in feathers of female than male GHA, suggesting the two sexes feed at similar trophic levels (Phillips et al., 2009a). Although wind was not an important predictor in my models, it is important to note that finer scale

differences in responses to this and other variables may be masked by the inherent error in geolocation and smaller sample sizes in some cases.

Finally, although I did not test explicitly for individual differences, in assessing model performance it was apparent that habitat preferences of some individuals differed substantially from the population mean. Similarly, stable isotope analyses indicate that GHA from Bird Island moult in a wide range of habitats, from Antarctic to subtropical latitudes, although the timing of moult is uncertain (Phillips et al., 2009a). I could not test for all known sources of variation between and within populations, but am aware that other factors such as age may play a role (Catry et al., 2006); future studies should formally test these effects (Chapter 5).

Although predictive models are increasingly used to identify suitable habitat for poorly-known populations, there is increasing evidence that for pelagic seabirds, they have poor transferability (Torres et al., 2015, this study) and so caution is needed when inferring key foraging areas for untracked populations. Furthermore, my results indicate that birds from different island groups may overlap with different threats. The conservation status of GHA has recently been upgraded to Endangered by IUCN, as several populations, including SG, are in decline. In contrast, numbers at PEI appear to be stable (Ryan et al., 2009; ACAP, 2010). Although incidental mortality in longline fisheries is believed to be a major cause of decline, GHA were more commonly recorded as bycatch in Patagonian toothfish *Dissostichus eleginoides* fisheries in the south Indian than Atlantic Ocean (Nel et al., 2002), and so it seems unlikely to account for regional differences in population trends. On the other hand, as GHA from the two populations target different dynamic habitats, there may be contrasting impacts of climatic change. In particular, the higher breeding frequency of birds from PEI than SG (Ryan et al., 2007) suggests that environmental conditions are more benign for the former during the non-breeding period. Future research should investigate the implications that spatial and habitat segregation has on the conservation and management of this and other threatened seabird populations.

3.5 Abstract

Many animals partition resources to avoid competition, and in colonially-breeding species this often leads to divergent space or habitat use. During the non-breeding season, foraging constraints are relaxed, yet the patterns and drivers of segregation both between and within populations are poorly understood. I modelled habitat preference to examine how extrinsic (habitat availability and intra-specific competition) and intrinsic factors (population, sex and breeding outcome) influence the distributions of non-breeding grey-headed albatrosses *Thalassarche chrysostoma* tracked from two major populations, South Georgia (Atlantic Ocean) and the Prince Edward Islands (Indian Ocean). Spatial segregation was greater than expected, reflecting distinct seasonal differences in habitat selection and accessibility, and avoidance of intra-specific competition with local breeders. Previously failed birds segregated spatially from successful birds during summer, when they used less productive waters, suggesting a link between breeding outcome and subsequent habitat selection. In contrast, I found weak evidence of sexual segregation, which did not reflect a difference in habitat use. These results indicate that the large-scale spatial structuring of albatross distributions results from interactions between extrinsic and intrinsic factors, with important implications for population dynamics. As habitat preferences differed substantially between colonies, populations should be considered independently when identifying critical areas for protection.

3. Intrinsic and extrinsic drivers of segregation

4 ESCAPING THE OLIGOTROPHIC GYRE: YEAR-ROUND MOVEMENTS, FORAGING BEHAVIOUR AND HABITAT USE OF MURPHY'S PETRELS

The data in this Chapter also appear in Clay T.A., Phillips R.A., Manica A., Jackson H.A., & Brooke M.deL. Escaping the oligotrophic gyre: year-round movements, foraging behaviour and habitat use of Murphy's petrels. *Marine Ecology Progress Series*, in review.

4.1 Introduction

Many species cover considerable portions of the earth's surface to take advantage of ephemeral food supplies (Dingle, 1996). In particular, pelagic seabirds have low movement costs and may undertake extensive trans-equatorial migrations in order to exploit seasonally productive areas (e.g. Shaffer et al., 2006; Guilford et al., 2009; Dias et al., 2011). In temperate and polar regions, predictable prey patches form around physical oceanographic features such as shelf- and ice-edges and upwellings (Weimerskirch, 2007), leading to large aggregations of seabirds and other marine predators (Block et al., 2011). In contrast, in tropical and subtropical oceans, the presence of a permanent thermocline prevents the

enrichment of surface layers and, as a result, primary production is generally low year-round (Ashmole, 1971; Longhurst and Pauly, 1987).

As their food resources are patchily distributed, tropical seabirds have evolved specific foraging adaptations that enable them to search large areas efficiently (Ballance & Pitman 1999). Many species have distinctive wing morphologies or feed in association with sub-surface predators such as tuna (Scombridae) or dolphins (Delphinidae) that drive prey to the surface (Au and Pitman, 1986; Spear and Ainley, 1998; Catry et al., 2009). For example, in the eastern tropical Pacific, selection for flight proficiency in terns (Sternidae) and petrels (Procellariidae) is associated with their use of less productive waters, reducing competition with larger species such as boobies *Sula* spp. that gather around schools of tuna in more productive regions (Ballance et al., 1997).

Whilst research efforts in tropical waters have increased over the last two decades (e.g. Ballance et al., 1997; Congdon et al., 2005; Jaquemet et al., 2005; Le Corre et al., 2012), little is known about the foraging ecology of seabirds in some of the ocean's least productive areas, the subtropical gyres, where the circulation of currents prevents upwelling of nutrients (Longhurst, 2007). In the North Pacific, Hawaiian albatrosses and other marine predators target the North Pacific Transition Zone (NPTZ), a highly productive region north of the North Pacific Gyre, between subarctic and subtropical water masses (Polovina et al., 2001; Hyrenbach et al., 2002; Kappes et al., 2010). In contrast, the South Pacific Gyre is permanently oligotrophic (Dandonneau et al., 2004), and much less is known about how the region's marine predators balance their energetic demands (Mannocci et al., 2014). Despite the impoverished oceanic environment, many islands support large populations of pelagic seabirds such as gadfly petrels, *Pterodroma* spp., a large group (34 species) of small to medium sized petrels which range in tropical to subantarctic waters. A large proportion of these species (76%) are classified by the International Union for the Conservation of Nature (IUCN) as threatened (Vulnerable, Endangered or Critically Endangered) or Near-Threatened, principally due to predation by introduced mammals at their breeding sites (BirdLife International, 2010). Knowledge of their at-sea distributions is primarily limited to shipboard observations, where data collection can be challenging as these highly pelagic birds are usually observed in very low densities (Spear et al., 2007), with the exception of a small minority of species tracked using miniature geolocators in recent years (Rayner et al., 2008; Pinet et al., 2011; Ramirez et al., 2013; Ramos et al., 2016; Nicoll et al., 2016). In the

Pacific Ocean, where the majority (21 of 34 species) breed (Brooke, 2004), there is published information on the movements of just five species, all confined to New Zealand and Australian breeding sites (MacLeod et al., 2008; Rayner et al., 2008, 2012, 2016; Priddel et al., 2014).

Henderson Island (24° 20' S, 128° 20' W; Fig. 4.1) is an uninhabited island of the UK Overseas Territory of the Pitcairn Islands and is one of the most important breeding sites in the world for gadfly petrels (Brooke et al., 2010). The island is the principal breeding site of the Henderson petrel *Pterodroma atrata* (> 95% of world's population), a major breeding site for Kermadec *P. neglecta* and Herald petrels *P. heraldica*, and holds populations of Murphy's *P ultima* and, possibly, Phoenix petrels *P. alba*. All species are thought to have been at much higher numbers before the arrival of Polynesians and introduction of the Pacific rat *Rattus exulans*, almost 1,000 years ago (Steadman and Olson, 1985; Brooke, 1995). Due to the paucity of studies on the movements of gadfly petrels from the subtropical South Pacific, very little is known about how these species use the marine environment, or at-sea threats.

Using miniaturised geolocators, the movements of Murphy's petrels were studied across two years. Unlike their sympatric congeners, Murphy's petrels breed during the austral winter, laying more or less synchronously, which facilitates device deployment and retrieval (Brooke, 1995). They have amongst the longest incubation shifts of any seabird, averaging 19.3 days; it has been suggested that breeding birds could travel as far as the California coast, where they have been observed in June and July (Bailey et al., 1989; Brooke, 1995). These particularly long trips may reflect the lack of available prey in the oligrotrophic environment around their breeding colonies, but their oceanographic habitat use is unknown. Initial dietary analysis suggests that birds might feed nocturnally on bioluminescent squid (Imber et al., 1995), yet few direct observations have been made of foraging birds.

Gadfly petrels are sexually monomorphic, yet tracking studies have revealed that males and females forage in distinct areas during pre-laying exodus (Pinet et al. 2012, Rayner et al. 2012). For example, male Barau's petrels Pterodroma barauii in the tropical Indian Ocean use more productive regions than females, possibly in preparation for their first long incubation stint, which is always taken by the male (Brooke 1995, Pinet et al. 2012). Given that Murphy's petrels have even longer incubation shifts, we might expect sex differences in energetic requirements early in the breeding period to be reflected in their foraging behaviour. In this study, I investigate, for the first time, the movements, activity patterns and

habitat use of Murphy's petrels during the breeding and non-breeding periods. In particular, I aimed to 1) define accurate breeding and migration schedules, 2) identify their main foraging grounds, 3) characterize marine habitats, 4) examine activity budgets, including the degree of nocturnal activity and 5) investigate sex-differences in movements, distributions and habitat use.

4.2 Methods

4.2.1 Study species and site

Murphy's petrel is a sexually monomorphic, surface-nesting species that breeds in the Pitcairn Islands and French Polynesia in the central South Pacific Ocean (Fig. 4.1). Fieldwork took place in July 2011 and July 2013 on Henderson Island where 2,500 ± 500 pairs breed (Brooke, 1995). Murphy's petrels suffer from chick predation by Pacific rats, usually within the first five days after hatching, and have very low breeding success (<10 %) (Brooke, 1995; Brooke et al., 2010). In August 2011, 75 tonnes of rodent bait were dropped by helicopter onto Henderson Island in an attempt to rid the island of Pacific rats (Torr and Brown, 2012). The operation caused massive rat mortality, however by 2013, rat numbers had recovered to near pre-eradication levels (Amos et al., 2016).

4.2.2 Geolocator tracking

Twenty-five geolocator-immersion loggers were deployed (Mk18H, British Antarctic Survey, Cambridge, UK) on incubating or brooding adults. In July 2013, 18 devices (72%) were retrieved and successfully downloaded, including from five pairs of birds. Loggers measured 17 x 10 x 6.5 mm and weighed 1.9 g, and were attached to a plastic ring on the tarsus. The mass of the logger, rings and cable tie was well below the limit recommended for flying seabirds (Phillips et al., 2003), based on a mass of 400-500 g for this species (Brooke, 1995). All birds except one were sexed using DNA from contour feathers. The exception was assigned as male since its partner was female. Colony attendance during incubation based on immersion data (see below) confirmed these sexes were accurate (Fig. 4.2).

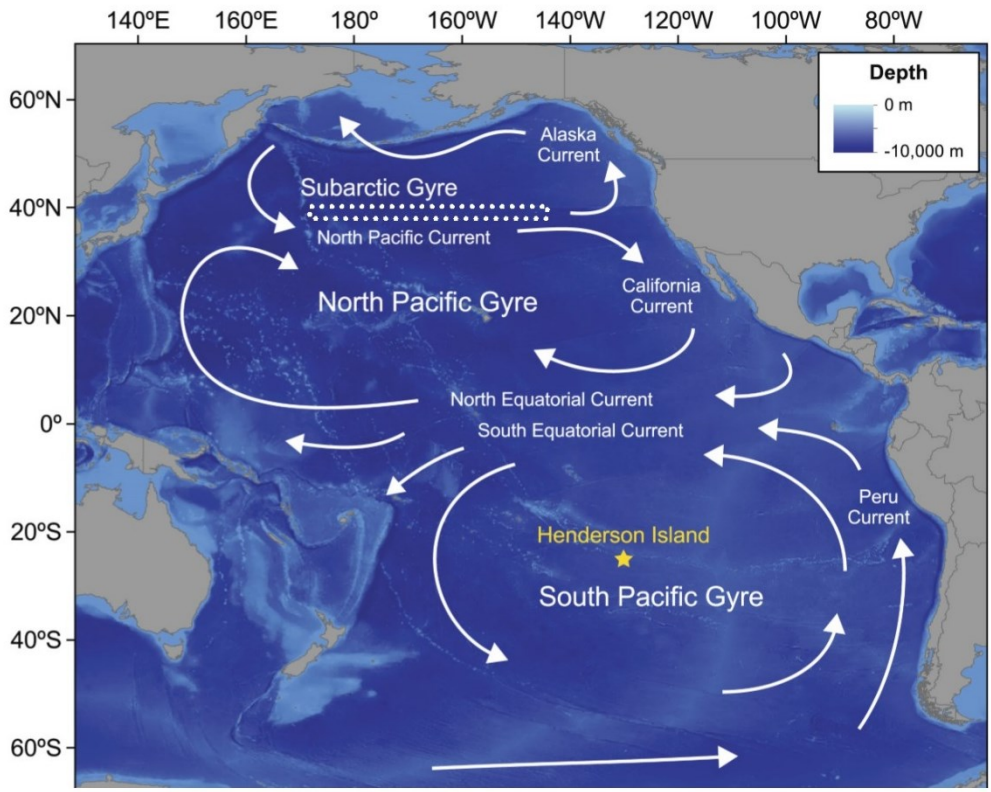


Figure 4.1. Map of the Pacific Ocean with bathymetry in blue shading and the positions of main ocean gyres and directions of currents in white text and arrows, respectively. The dotted white box demarcates the rough position of the North Pacific Transition Zone (NPTZ).

Loggers sampled light every minute, recording the maximum value every five minutes (Afanasyev, 2004). Light data were processed using the BASTrak software suite (British Antarctic Survey, Cambridge, UK) based on the timings of sunrise and sunset determined from thresholds in the light curves. Latitude is derived from the daylight length and longitude from the timing of local midday relative to Greenwich Mean Time and day of the year, providing two locations per day with a mean accuracy of 186 ± 114 km in pelagic seabirds (Phillips et al., 2004b). I removed locations derived from light curves with obvious interruptions around dawn or dusk, and periods around the equinox (2 to 4 weeks), when latitude cannot be estimated reliably. The loggers also tested for saltwater immersion every 3 s, storing the sum of positive tests (between 0 and 200) at the end of each 10 min period, with each period categorized as daylight or darkness based on the light recorded by the logger, which corresponded approximately to civil twilight.

As nests could not be monitored during the study period, I assigned breeding stage and phenology based on a combination of movements and activity patterns (Guilford et al., 2012). Routes taken to and from non-breeding areas could not be determined because birds migrated during equinox periods. I assumed that over the study period, hatchling survival was low, and as it was challenging to assign early chick-rearing trips using immersion data, even within pairs (Fig. 4.2), I made no attempt to assign breeding success to tracked birds. Consequently, movements from the end of incubation to migration are classed as 'late breeding'. This period was removed from analysis of activity patterns, as it was not clear whether dry periods represented time spent at the colony or flying, whereas this distinction is obvious during incubation.

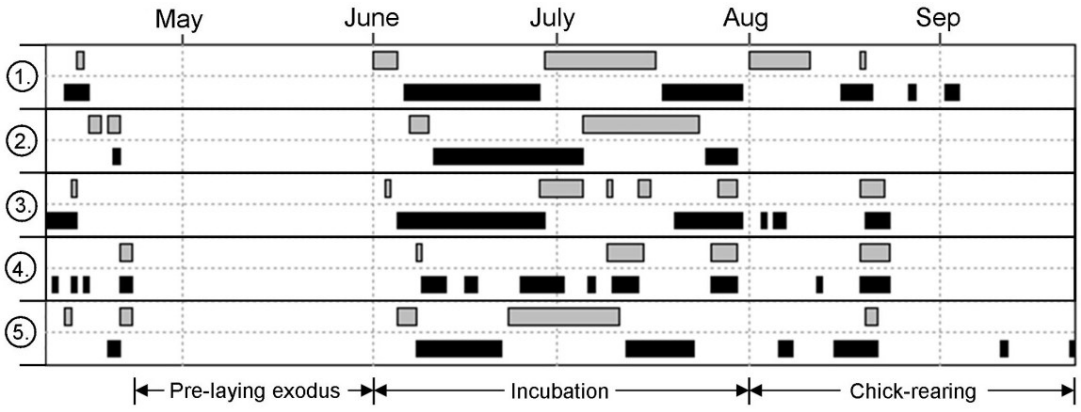


Figure 4.2. Attendance patterns in five pairs of Murphy's petrels during the 2012 season, determined from immersion data. Females are shown with grey shading and males with black shading, and each pair is numbered. Birds return to the colony in mid-late April, before engaging in a pre-laying exodus. Females return slightly earlier to lay the egg, which precedes a male-female-male pattern of progressively shorter incubation shifts. Brooding occurs immediately after hatching (late July to mid-August). The fates of the chicks were unknown.

I calculated maximum ranges and cumulative distances using great circle distances in the R package *fields* (Nychka et al., 2016). As birds appeared to use two main foraging strategies during incubation, I classified long looping trips eastwards as 'east' and shorter trips south as 'south'. I investigated the influence of sex and year differences on movement characteristics and timings of key events (see Table A3.1), within a generalized linear mixed-effects model (GLMM) framework in the lme4 package in R (Bates et al., 2015). I used a Gaussian error structure for all models except for incubation trip type (east or south), where a binomial

structure was used. I included sex, year, and their two-way interaction as covariates, as well as the random effect of individual identity. For models comparing incubation duration, and cumulative and maximum distance travelled, I included trip type as a fixed effect along with sex and year. For all model comparisons, Akaike Information Criterion (AIC) values were used to rank all possible model combinations according to their degree of parsimony. Where multiple models were within 2 AIC units of the best supported model, the most parsimonious model was chosen (Burnham and Anderson, 2004; Arnold, 2010).

I created utilization distribution (UD) kernels to compare patterns of space use across the annual cycle. Plots of the increase in kernel area with isopleth level for each individual and stage indicated that the 50% kernel was the most appropriate for cross-stage comparisons of core areas. The 95% kernel was considered to represent the general use area. To control for differences between individuals, separate UDs were generated for each bird, and then merged to ensure equal representation for the population. I selected a grid size of 50 km and smoothing parameter of 200 km to account for geolocator error (Phillips et al., 2004b, 2005). I investigated whether space use differed between sexes and years for each breeding stage. I calculated observed overlap in core and general use areas using Bhattacharyya's affinity (BA), which is the most appropriate measure of quantifying similarity among UD estimates (Fieberg and Kochanny, 2005). This was done using the *kerneloverlap* function in the R package *adehabitatHR* (Calenge, 2006). BA estimates range between 0 to 1, representing no similarity between UDs (or overlap) and identical UDs (or complete overlap), respectively. I used a randomization procedure to test the null hypothesis that there was no difference in spatial distributions. To test for differences in sex and year, I randomly reassigned bird identities without replacement and calculated overlap scores for 1000 iterations, maintaining the same ratios observed. *P*-values were determined as the proportion of randomized overlaps that were smaller than the observed (Breed et al., 2006).

4.2.3 Habitat use

I compared habitat characteristics in the core and general use areas by overlaying the density contours with maps of bathymetry and remotely-sensed sea surface temperature (SST) and chlorophyll *a* concentration (Chl *a*). Bathymetry was obtained from NOAA's ETOPO 1 min resolution dataset (http://www.ngdc.noaa.gov/mgg/global/etopo2.html). Aqua MODIS SST and Chl *a* were downloaded as monthly, 9km resolution composites from the Oceancolor

website http://oceancolor.gsfc.nasa.gov/) using the Marine Geospatial Ecology Tools extension in ArcGIS 10.1 (Roberts et al., 2010). I averaged monthly composites for each breeding stage and extracted the median value within the 50% and the area between the 50 and 95% kernel isopleths for each individual. I initially ran a set of GLMMs testing for the effect of breeding stage, sex and isopleth level (core or general use) and their interactions for each variable. However, because of the difficulties of interpreting high order interactions, separate models were then generated for each breeding stage. As a result, I constructed models for each environmental variable (Chl *a*, SST and bathymetry) and stage, with individual identity as a random effect, testing the effects of year, sex and isopleth level (core or general use), as well as the interaction between sex and isopleth level. I used an information criterion approach (see above) to select the best model. Finally, in order to assess annual movements in relation to seasonal changes in chlorophyll, I calculated 8-day climatologies of Chl *a* averaged over a ten year period from 2004 to 2013 to control for annual differences in oceanography, such as those caused by El Niño-Southern Oscillation events (Bograd et al. 2004). I extracted Aqua MODIS Chl *a* for the breeding and non-breeding ranges (95% kernels) using the xtractomtatic routine (http://coastwatch.pfel.noaa.gov/xtracto/), enabling data extraction from the BloomWatch website (http://coastwatch.pfel.noaa.gov/coastwatch/CWBrowserWW360.jsp). Climatologies are presented for each region as means ± SD (See Fig. 4.6).

4.2.4 Activity analysis

I selected three measures of activity that reflect at-sea foraging and flight behaviour of petrels in daylight and darkness (Spear et al., 2007): proportion of time spent on the water, duration of flight bouts in minutes and number of landings per hour. As the activity data are binned into 10 minute periods, it is possible that the number of wet or dry bouts is underestimated. However (Phalan et al., 2007) found a high correlation between immersion data binned in this way, and data collected at higher resolution, indicating that the former provide reasonable measures of activity. Immersion data were recorded from two individuals for less than six months and were excluded from activity analyses.

Activity data were split by breeding stage, excluding dry periods spent at the colony, and daily patterns were compared between stages, year and daylight *vs.* darkness (a categorical variable) using GLMM with individual identity as a random effect. To increase normality of

distributions, I square-root transformed number of landings per hour, log-transformed flight bout durations, and arcsine-transformed the proportion of time spent on water. I tested the importance of all combinations of predictors and their interactions using AIC values (as above). Observed means are reported ± SD and modelled parameter estimates are reported ± SE. The observed means are given in tables to enable comparisons with other studies (as in Mackley et al., 2010). All analyses were conducted in the software R v. 3.1.1 (R Core Team, 2014), unless otherwise stated.

4.3 Results

4.3.1 Distribution and annual cycle

Murphy's petrels showed clear separation between breeding and non-breeding grounds, when they used the South and North Pacific, respectively (Fig. 4.3). During the pre-laying exodus, birds foraged south and southwest of the colony around the Subtropical Convergence, east of the Chatham Rise (50% UD, 160 - 115°W, 25 - 50°S; Fig. 4.3b). There was clear sexual segregation during this period in both the core (50% UD; observed overlap 0.08 and randomized overlap 0.23 ± 0.06, $P < 0.019$; Fig. 4.4b; Table 4.1), and general use areas (95% UD; observed overlap 0.72 and randomized overlap 0.82 ± 0.04, $P < 0.023$; Fig. 4.4b; Table 4.1), but no differences between sexes in mean longitudes or latitudes (Table A3.1). Males ranged further from the colony (3,826 ± 449 km) than females (2,921 ± 634 km), but did not cover greater distances or differ in timing of movements (Table A3.1). Birds departed from, and returned to the colony significantly earlier in 2013 (18 April ± 7 days and 4 June ± 6 days) than in 2012 (26 April ± 7 days and 10 June ± 6 days), and as a result the duration of the pre-laying exodus was marginally shorter (47 ± 3 days in 2012 and 45 ± 3 days in 2013, Table A3.1). I found no evidence of sexual segregation during any other stages of the annual cycle in either core or general use areas (Table 4.1, Fig. 4.4). Nor did I find evidence of differences in these distributions between years (Table 4.1).

During incubation, birds foraged over large areas of subtropical waters south and east of the colony (50% UD, 140 - 80°W, 10 - 45°S; Fig. 4.3c). Females departed for, and returned from, their first incubation trip earlier (11 June ± 6 days and 1 July ± 7 days) than males (27 June ± 7 days and 14 July ± 7 days), showing males took the first incubation shift (Fig. 4.2); however, their trip durations were not significantly different (20 ± 5 days and 18 ± 4 days,

respectively, Table A3.1). First incubation trips were significantly longer in 2012 than 2013 (20 ± 3 days and 17 ± 5 days, respectively, Table A3.1). For three birds I identified a second incubation trip in 2012 (departing on 19 July ± 8 days and returning on 2 August ± 8 days); these second trips appeared to be shorter (14 ± 3 days, n = 3) than first trips, but the small sample precluded a statistical comparison. I classified incubation trips into either short trips south (29%; 2012 n = 5, 2013 n = 4) or long looping trips east (68%; 2012 n = 13, 2013 n = 8) of the colony, except one (2012) which was a long looping trip (19 d) west of the colony.

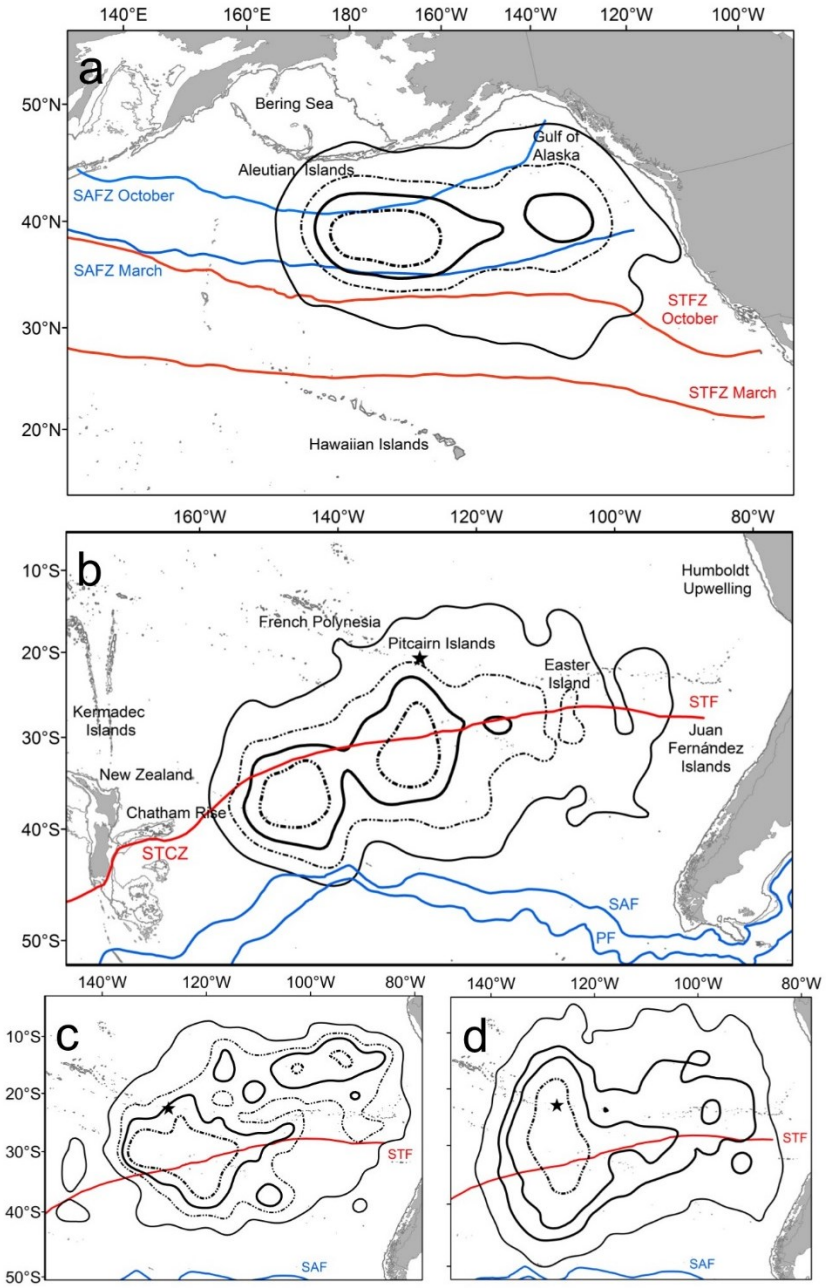


Figure 4.3. The 25% (dashed), 50% (solid), 75% (dashed) and 95% (solid) utilisation distributions (UDs) of Murphy's petrels tracked with geolocator-immersion loggers are shown during a) non-breeding, b) pre-laying exodus, c) incubation, and d) late breeding. In the North Pacific, the positions of the Subtropical Front (STF, red) and Subarctic Front (SAF, blue) were generated from isotherms for the first (October) and last (March) months of non-breeding (based on Hyrenbach et al. 2002), whereas in the South Pacific the positions of fronts are year-round averages. STFZ - Subtropical Frontal Zone. SAFZ - Subarctic Frontal Zone. SAF – Subantarctic Front. PF – Polar Front. STCZ – Subtropical Convergence Zone.

Table 4.1. Observed and randomized overlap (Bhattacharyya's affinity, BA) of core (50%) and general use (95%) utilization distributions (UDs) of Murphy's petrels tracked with geolocator-immersion loggers in 2011/12 and 2012/13, compared between years and sexes in each breeding stage.

	50%			95%		
Class	Observed	Randomized	*P*	Observed	Randomized	*P*
Sex	-	-	-	-	-	-
Non-breeding	0.28	0.30 ± 0.05	0.36	0.90	0.89 ± 0.03	0.75
Pre-laying exodus	0.08	0.23 ± 0.06	**0.019**	0.72	0.82 ± 0.04	**0.023**
Incubation	0.15	0.17 ± 0.04	0.23	0.72	0.77 ± 0.05	0.14
Late breeding	0.29	0.33 ± 0.02	0.058	0.88	0.88 ± 0.02	0.33
Year	-	-	-	-		
Non-breeding	0.27	0.30 ± 0.05	0.28	0.89	0.89 ± 0.03	0.63
Pre-laying exodus	0.25	0.23 ± 0.06	0.69	0.83	0.82 ± 0.04	0.57
Incubation	0.24	0.17 ± 0.04	0.99	0.83	0.77 ± 0.05	0.99
Late breeding	0.31	0.33 ± 0.02	0.19	0.88	0.89 ± 0.02	0.44

Sexes are pooled for year comparisons and vice versa. Randomized overlaps are shown as a median ± interquartile range. P represents the proportion of randomized overlaps that were smaller than the observed. Significant differences are shown in bold.

Trip duration was not influenced significantly by trip type (Table A3.1), however birds that took trips east travelled further (east trips 14,527 ± 3,548 km, south trips 10,158 ± 4,078 km) and ranged further from the colony (south trips 2,012 ± 600 km, east trips 3,757 ± 829 km, Table A3.1). Trips east were predominantly in an anti-clockwise looping pattern (although one eastward trip of 21 days was clockwise), appearing to take advantage of trade winds in the southeast Pacific, particularly for the return journey (Fig. 4.5). Birds tended to travel southeast to the Subtropical Front and then northeast past Easter Island to an area off the Humboldt Upwelling west of Peru, around 3,500 km east of Henderson Island. Maximum distances from the colony were 4,161 km in 2012 and 4,898 km in 2013. Trips south were generally 1,000 km southeast or southwest of the colony and appeared to target the Subtropical Front (Fig. 4.3c, Fig. 4.5).

Although I could not determine from activity or movements whether birds tracked after hatching retained a chick, the last dry night at the colony did not differ between years (25 August ± 18 days; Table A3.1), suggesting a similar pattern of colony attendance in 2011 and 2012. During this period, birds foraged closer to the colony than during incubation, sometimes using an area in the southeast Pacific towards northern Chile (50% UD 140 - 95°W, 15 - 50°S; Fig. 4.3d).

There were no significant effects of year on any of the migration metrics (Table A4.1). Birds migrated northwest across the Pacific, departing the eastern South Pacific on 22 October ± 18 days and arriving at the western edge of their non-breeding grounds in the central North Pacific, over 8,000 km from Henderson Island on 3 November ± 27 days. Whilst in the North Pacific, Murphy's petrels used two core areas at approximately 40 - 45°N, one south of the Aleutian Islands around the Subarctic Front (175 - 155°W), and the other further east, south of the Gulf of Alaska (145 - 135°W) (Fig. 4.3a). In the 2011/12 season, the petrels were distributed significantly further north (by 0.9°) than in 2012/13, possibly the result of inter-annual variability in the position of the NPTZ (Fig. A3.2). The residency period in the North Pacific lasted 154 ± 27 days, after which birds departed on 6 April ± 15 days, travelling almost directly south, returning to the South Pacific on 17 April ± 18 days and spending the first night at the colony on 18 April ± 16 days. There was no difference in the duration of outbound and return trans-equatorial migrations (GLMM, best fitting model, 10 ± 3 days and 11 ± 4 days, respectively).

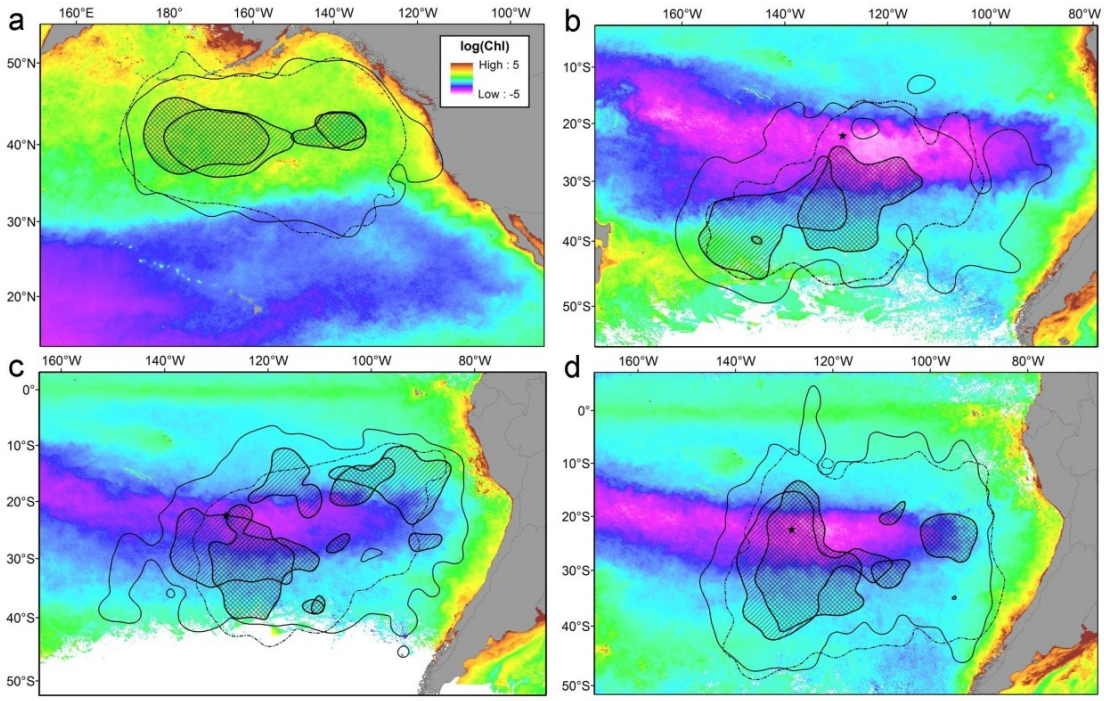


Figure 4.4. Core (50%) and general use (95%) utilisation distributions (UDs) of male (hatched fill and solid lines, respectively) and female (cross-hatched fill and dashed lines, respectively) Murphy's petrels tracked during a) non-breeding (October-March), b) pre-laying exodus (April-May), c) incubation (June-July) and d) late-breeding (August-September). The log of chlorophyll *a* concentration (mg m^{-3}) is shown averaged across the period of interest.

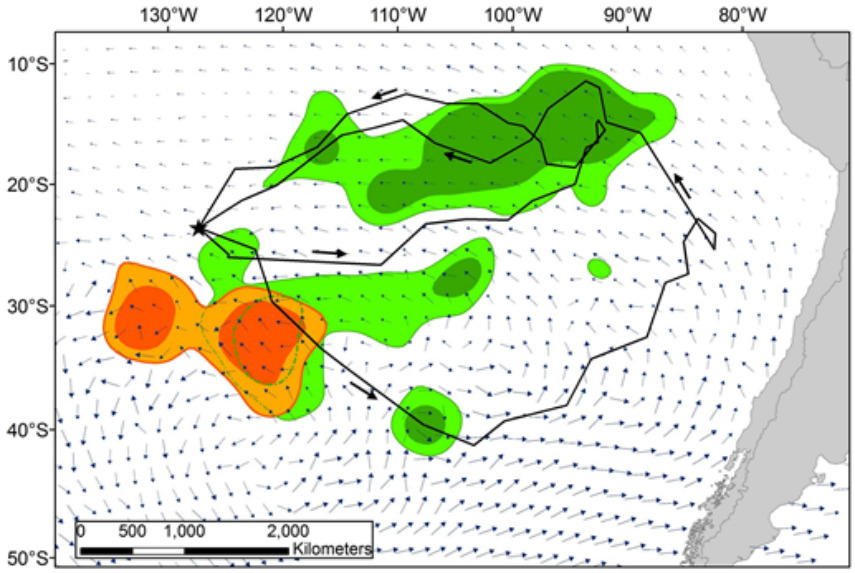


Figure 4.5. Incubation strategies of Murphy's petrels tracked with geolocation-immersion loggers in relation to wind regimes. The 25% and 50% UDs are shown for birds that undertook trips south (dark and light orange, respectively) of the colony and looping trips east (dark and light green, respectively) east of the colony towards the Humboldt Current. Examples of two looping trips are shown as black lines with black arrows indicating their direction. The averaged monthly wind speed and direction over the incubation period (June – July) are shown with blue arrows, with higher speeds represented by longer arrows.

4.3.2 Habitat use

Although Murphy's petrels did not appear to target the most productive areas of the Pacific Ocean, the tracked birds timed their movements to use their non-breeding and breeding ranges when at their most productive (Fig. 4.6). The petrels used deep (> 3,000 m) pelagic waters across the annual cycle, particularly during non-breeding (50% UD, 5,124 ± 495 m) (Table 4.2). Birds used a range of subtropical waters (15°C - 20°C) of oligotrophic (Chl *a* < 0.1 mg m^{-3}) and mesotrophic productivity during breeding and the pre-laying exodus, respectively, and colder subarctic waters of much higher productivity during non-breeding (Fig. 4.4).

On average, core areas were significantly deeper than the rest of the range in all stages except non-breeding (Table 4.2, A3.3). Core waters were significantly cooler than peripheral waters during both the non-breeding (50% UD 9.5 ± 1.4°C) and pre-laying exodus (50% UD 15.6 ± 1.4°C) (Table 4.2, A3.3), corresponding to areas around and to the north of the Subarctic Front, and around and to the south of the Subtropical Front, respectively. There were no differences in water temperature between core and general areas during incubation and late breeding (Table 4.2). During pre-laying and late breeding, core areas were associated with higher chlorophyll values than general use areas, while there was no difference during incubation or non-breeding (Table 4.2, A3.3). There were sex differences in bathymetry and productivity values during the pre-laying exodus when males used waters with higher chlorophyll concentrations and of greater depth than females, but with no differences in sea surface temperatures (Table 4.2, Fig. 4.4b). During late breeding, despite there being no evidence of spatial segregation, females were associated with higher chlorophyll concentrations (Table 4.2, Fig. 4.4d).

Table 4.2. Habitat characteristics within individual core (0-50%) and between core and general use (51-95%) utilisation distributions (UDs) of Murphy's petrels tracked with geolocator-immersion loggers in 2011/12 and 2012/13, for each sex and breeding stage.

	Chlorophyll (mg m-3)		Sea surface temperature (°C)		Depth (m)	
	0-50%	51-95%	0-50%	51-95%	0-50%	51-95%
Non-breeding						
Male	0.29 ± 0.01	0.29 ± 0.03	9.8 ± 1.4	10.3 ± 2.3	-5112 ± 480	-5041 ± 367
Female	0.30 ± 0.01	0.29 ± 0.02	9.1 ± 1.3	10.5 ± 2.0	-5145 ± 539	-5101 ± 160
Pre-laying exodus						
Male	0.11 ± 0.04	0.08 ± 0.02	15.2 ± 2.1	17.3 ± 1.9	-4762 ± 524	-4409 ± 454
Female	0.08 ± 0.03	0.07 ± 0.02	16.2 ± 2.9	18.2 ± 1.5	-4160 ± 498	-3980 ± 284
Incubation						
Male	0.09 ± 0.02	0.08 ± 0.02	20.4 ± 3.3	20.2 ± 2.7	-3919 ± 315	-3824 ± 280
Female	0.09 ± 0.02	0.08 ± 0.02	18.4 ± 3.6	18.4 ± 3.3	-3822 ± 179	-3710 ± 232
Late breeding						
Male	0.07 ± 0.02	0.09 ± 0.02	18.2 ± 2.5	18.6 ± 2.5	-3950 ± 239	-3845 ± 185
Female	0.09 ± 0.02	0.09 ± 0.02	17.8 ± 2.9	18.4 ± 2.1	-3886 ± 213	-3727 ± 82

Values were averaged across both years of tracking and are presented as means ± SD. Horizontal and vertical lines indicate significant differences between isopleth levels and sexes, respectively. Interactions between sex and isopleth level were not significant, thus isopleth differences are for both sexes combined and vice versa.

4.3.3 Activity patterns

Activity patterns varied considerably during the annual cycle (Fig. 4.7). The best fitting models explaining variation in all four metrics contained the influence of daylight or darkness, breeding stage and the interaction between daylight or darkness and breeding stage, while the best fitting model explaining the duration of flight bouts also included the fixed

effect of year (Table A3.2). The greatest amount of time spent sitting on the water was during the non-breeding period, followed by the outward and return migrations, pre-laying, and incubation periods (Table 4.3, Fig. 4.7). In contrast, landing rate was greatest during incubation and least during non-breeding (Table 4.3). Non-breeding petrels landed more often and had longer flight bouts during daylight. During outward and return migrations, pre-laying exodus and incubation, petrels landed more often during daylight, but had longer flight durations during darkness. Large standard deviations in flight bout durations during incubation indicate substantial individual variation. During pre-laying exodus and non-breeding, birds spent a greater proportion of time on the water at night, whereas during the other stages, birds spent a greater proportion of time wet during daylight. Flight bout durations were slightly (around 3 min) longer during non-breeding, outward migration and pre-laying exodus (Fig. A3.1). Finally, year explained a negligible degree of variation in activity patterns (Fig. A3.1).

Diel activity patterns were apparent in all breeding stages, with birds increasing flight activity up to two hours before dawn, and around sunset (Fig. 4.8). During non-breeding, diel behavioural changes were particularly pronounced with birds reducing the time they spent on water from 60% to 15% before dawn, exhibiting high flight activity up to four hours after dawn.

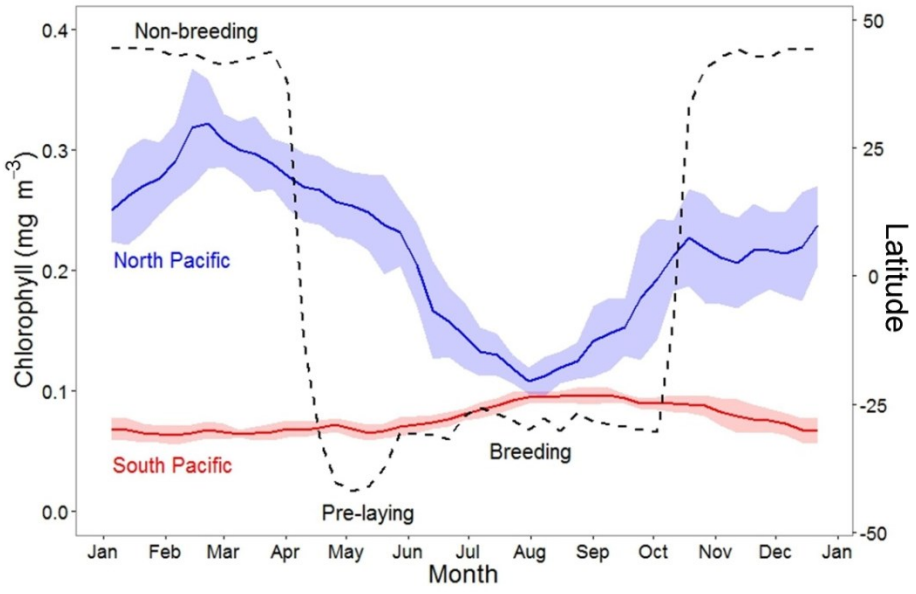


Figure 4.1. Murphy's petrel latitudinal movements and ocean productivity in the South (red) and North (blue) Pacific throughout the year. Productivity (left y-axis) is presented by the mean ± SD of 8-day chlorophyll a concentrations from 2004 to 2013, encompassing the breeding and non-breeding ranges (95% UD). Latitudes (right y-axis) are presented as an average of weekly individual means.

Table 4.3. Summary of activity patterns of Murphy's petrels tracked with geolocator-immersion loggers for each stage of the annual cycle.

	Time on water (%)		No. landings (h-1)		Duration of flight bouts (min)	
	L	D	L	D	L	D
Outward migration	26 ± 13	18 ± 14	0.83 ± 0.16	0.65 ± 0.19	54.5 ± 7.0	79.5 ± 20.0
Non-breeding	45 ± 4	62 ± 6	0.71 ± 0.06	0.41 ± 0.07	46.7 ± 4.5	44.5 ± 3.1
Return migration	27 ± 11	20 ± 22	0.81 ± 0.10	0.58 ± 0.18	57.6 ± 5.9	82.6 ± 20.3
Pre-laying exodus	11 ± 7	14 ± 8	0.99 ± 0.08	0.87 ± 0.09	56.3 ± 7.7	59.2 ± 8.4
Incubation	6 ± 4	3 ± 4	1.03 ± 0.17	0.76 ± 0.15	57.6 ± 17.9	81.9 ± 22.9

Values are shown as means ± SD of individual averages for daylight (L) and darkness (D) separately. Model summaries and parameter estimates are shown in the Appendix 3.

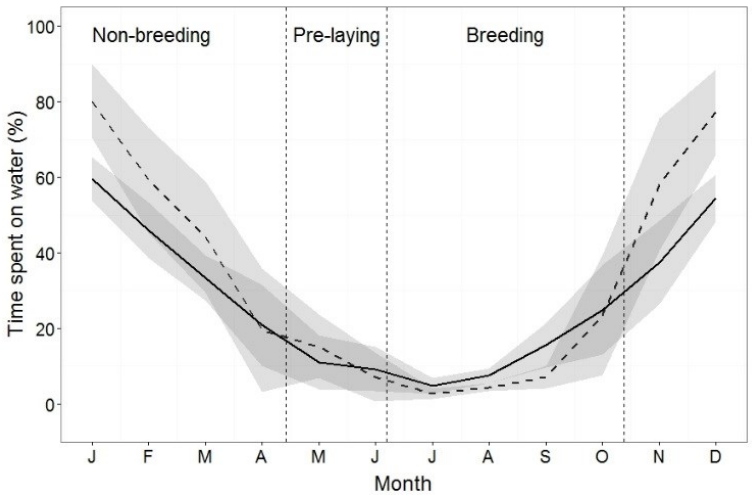


Figure 4.2. Annual variation in the percentage of time Murphy's petrels tracked with geolocator-immersion loggers spend on water in daylight (solid line) and darkness (dashed line). Means of individual monthly averages are shown ± SD.

4.4 Discussion

4.4.1 Year-round distribution and habitat use

Few studies have investigated the spatial ecology of gadfly petrels (but see Rayner et al., 2008; Pinet et al., 2011; Nicoll et al., 2016; Ramos et al., 2016), and none from the central Pacific Ocean, where there are several endemic species. This study reports, for the first time, the movements, foraging behaviour and habitat use of Murphy's petrel. The tracked birds used distinct areas throughout the annual cycle, remaining in the South Pacific when breeding, and conducting trans-equatorial migrations to the North Pacific during non-breeding. There are few sightings of Murphy's petrels from ship-based surveys, including small numbers observed off the coast of California and in the eastern tropical Pacific (Bartle et al., 1993; Haney et al., 1995; Spear et al., 2007). Given the chronological sequence of observations off California (April – June), in the Gulf of Alaska (July) and in the Hawaiian archipelago (September – November), Bartle et al., (1993) suggested that this species performed anti-clockwise movements through the North Pacific during breeding. However direct observations of the northward track of birds off Hawaii and the freshly-moulted plumage of birds off California led Howell (2012) to suggest a clockwise transit through the North Pacific during non-breeding, similar to that here described.

Energetic demands increase during breeding, and many seabirds select the most productive habitats (e.g. Péron et al., 2010). Murphy's petrels breed in the middle of the South Pacific Gyre, where ocean currents are relatively weak and there is minimal upwelling of deep water and, as a result, consistently low primary productivity (D'Hondt et al., 2009). These results indicate that Murphy's petrels have adapted to breeding in the 'largest oceanic desert' (Claustre and Maritorena, 2003) by travelling vast distances to forage at the southern and eastern edges of the gyre. Birds depart on long pre-laying trips (46 ± 3 days), characteristic of *Pterodroma* spp. (Warham, 1990). Interestingly, males and females use mutually exclusive foraging areas with different habitat characteristics; males use deeper and more productive waters downstream of the Chatham Rise, whilst females appear to target the Subtropical Frontal Zone. In many seabirds, sexual segregation during breeding is attributed to size-mediated competitive exclusion or niche divergence (Shaffer et al., 2001b; Phillips et al., 2004a, 2011). However, Murphy's petrels are sexually monomorphic and do not appear to segregate at sea during incubation or chick-rearing. Therefore, pre-laying segregation may be

related to different energetic requirements or reproductive roles in the early breeding season (Hedd et al., 2014; Quillfeldt et al., 2014). Similar pre-laying segregation is observed for Barau's petrels *Pterodroma barauii* (Pinet et al., 2012) and Chatham Petrels *P. axillaris*(Rayner et al., 2012) where males also travel further from the colony to more productive areas, suggesting that this behaviour might be common among gadfly petrels. Further research should investigate if segregation is indeed driven by dietary or habitat requirements.

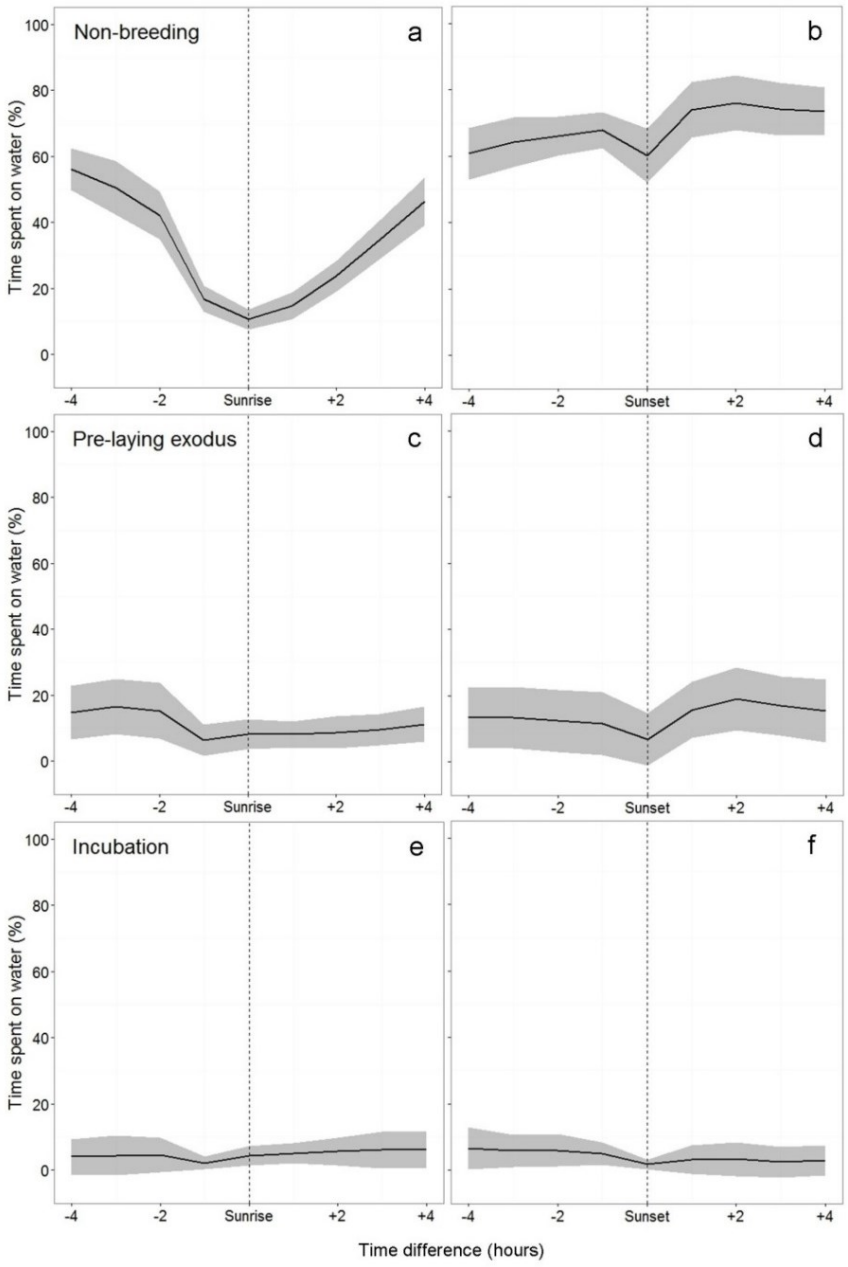


Figure 4.3. Diel variation in the proportion of time spent on water by Murphy's petrels during (a and b) non-breeding, (c and d) pre-laying exodus and (e and f) incubation. For each breeding stage, day length and the duration of twilight vary according to differences in latitude and calendar date. As a result, activity budgets are presented as the number of hours before and after (left) sunrise and (right) sunset, derived light data recorded by geolocators. Hourly means were averaged for each individual and day and are shown (± SD).

One of the most striking results of this study was the great distance travelled by Murphy's petrels during incubation trips, which appears to be the largest range of any seabird during breeding (reviewed in Pollet et al., 2014). As Murphy's petrels are known to have some of the longest incubation shifts (Warham, 1990; Brooke, 1995), they were predicted to range far from the colony; indeed, the maximum distance recorded (4,898 km) is similar to the maximum estimate of 4,600km made by (Brooke, 1995). As trip duration is often linked to prey density (e.g. Hamer et al., 2007), these long trip durations by Murphy's petrels might imply that they forage on scarce or unpredictable prey. However, the tracked birds appeared to use two discrete foraging areas, the Subtropical Front to the south, and an area east of the colony towards the Humboldt Current. Individuals conduct long looping trips southeast of the colony, and by following trade winds appear able to cover larger distances (Weimerskirch et al., 2005). Although more productive than the Gyre (Fig. 4.4), these are not the most productive areas in the South Pacific (Ballance et al., 2006). Birds perhaps avoid the latter, including the eastern tropical Pacific, to reduce competition with other seabirds (Ballance et al., 1997; Rayner et al., 2016). Possibly for the same reason, Murphy's petrels appear to overlap little with other gadfly species that spend the austral winter in the southeast Pacific (Rayner et al., 2011, 2012).

Murphy's petrels may also target the edges of the gyre due to specific habitat or dietary requirements. In areas offshore or downstream from upwellings, convergence zones form where upwelled water sinks below warmer surface waters, leading to aggregations of mesopelagic prey (Polovina et al., 2001; Saba et al., 2008). Indeed, the eastern region of the South Pacific Gyre is used extensively by leatherback turtles *Dermochelys coriacea* targeting zooplankton such as jellyfish (Saba et al. 2008, Shillinger et al. 2011). Mesopelagic prey are thought to be a dominant component of food webs in deep, oceanic waters (Ashmole, 1971), and often perform diel vertical migrations (DVM) to the sea surface at night (Hays, 2003),

making them available to air-breathing predators such as turtles or seabirds (Regular et al., 2010; Shillinger et al., 2011). Analysis of Murphy's petrel diets during chick-rearing has indicated they feed predominantly on bioluminescent squid, emphasizing their reliance on DVM prey (Imber et al., 1995).

All procellariform species that breed outside the tropics and routinely cross the Equator on migration, have a relatively synchronous laying period (Brooke 2004). As Murphy's petrels lay synchronously, in contrast to the other *Pterodroma* spp. on Henderson Island (Brooke 1995), the association between breeding period and migration pattern, suggests that the annual cycle is timed to coincide with seasonal peaks in food availability in the breeding or nonbreeding range (Fig. 4.6). By visiting the North Pacific during the boreal winter, Murphy's petrels avoid competition with millions of shearwaters in the summer (Shaffer et al., 2006; Hedd et al., 2012). This might also explain the winter breeding schedule of the Providence petrel *Pterodroma solandri*, which migrates from the southwest Pacific to the northwest Pacific off Japan (Brooke, 2004).

The North Pacific Transition Zone Chlorophyll Front (TZCF) is an area of high primary productivity spanning the subarctic and subtropical frontal zones, and is an important foraging and migration habitat for many marine predators (Polovina et al., 2001; Robinson et al., 2012). During winter, the TZCF moves progressively south, closer to colonies of breeding Hawaiian albatrosses, with which Murphy's petrels partly overlap (Polovina et al., 2015; Thorne et al., 2015). During winter and spring, strong westerlies cause mixing of nutrient rich waters and help maintain productivity in the absence of sunlight (Bograd et al., 2004). The TZCF is known to aggregate mesopelagic prey, in particular ommastrephid squids, which seasonally migrate from spawning areas in the subtropics to the subarctic frontal zone to feed on myctophid fishes (Watanabe et al., 2004; Ichii et al., 2009). I found that from February onwards in both years, Murphy's petrels moved eastwards towards the Gulf of Alaska and the California Current, appearing to take advantage of spring blooms in productivity before migrating back to the South Pacific (Fig. A3.2). This suggests that Murphy's petrels likely track dynamic features such as frontal zones, as do other procellariids (Kappes et al., 2010; Clay et al., 2016) . However, this needs to be confirmed by dynamic habitat modelling.

4.4.2 Year-round foraging behaviour

The Murphy's petrels adjusted their activity patterns across the annual cycle relative to the degree of central place constraint (Mackley et al., 2010, 2011). Birds spent more time flying during breeding, peaking at 95% of time at sea during incubation (Table 4.3). Indeed, Murphy's petrels are one of the most active seabirds, to my knowledge more so than any other small petrel (Rayner et al., 2012; Navarro et al., 2013; Ramirez et al., 2013; Dias et al., 2016), presumably reflecting the need to commute to distant foraging grounds. The high frequency of landings during incubation suggests that birds forage continuously on route. As foraging strategies of seabirds are a function of their marine environment (Weimerskirch, 2007), the extreme activity of Murphy's petrels is also likely to be related to the unpredictability of prey in the South Pacific, with birds searching at large scales, as in similar habitats elsewhere (Weimerskirch et al., 2005), but with even less time resting at the surface after prey capture. During non-breeding, Murphy's petrels spend much more time on the water, with reduced flight activity. Energy requirements are probably lower, yet during this period they also moult flight feathers which is an energetically demanding process. Indeed, recent studies have documented a quasi-flightless period associated with moult (Cherel et al., 2016; Gutowsky et al., 2014a). Although very little is known about feather moult in Murphy's petrels, gadfly petrels perform a simple descendent moult, replacing primary feathers sequentially over a period of 3-4 months (Bridge, 2006). As Murphy's petrels decrease their flight activity substantially from November-February (Fig. 4.6), it is likely this period of relative inactivity coincides with moult (Cherel et al., 2016), supported by observations of fresh plumage in birds at sea in April-May (Howell, 2012).

Whilst many gadfly petrels are known to be predominantly nocturnal (Brooke and Prince, 1991; Rayner et al., 2012; Ramirez et al., 2013; Dias et al., 2016), the night-time activity of Murphy's petrels appears to be related to commuting rather than feeding behaviour, as in darkness during migration and incubation, birds land less often and, during migration only, have significantly longer flight bouts. In contrast, during stages when birds commute shorter distances (pre-laying and non-breeding), they spent more time on the water at night. Although this could reflect a sit-and-wait foraging strategy seen in many albatrosses and larger petrels (e.g. Catry et al., 2004; Mackley et al., 2010), there are peaks in flight activity at dawn and dusk, suggesting that Murphy's petrels are predominantly crepuscular and diurnal rather than nocturnal foragers (Imber et al., 1995). The tracked birds consistently

began to fly more in the hour or two before sunrise and at sunset (Fig. 4.8), consistent with the hypothesis that they and other subtropical and tropical species rely heavily on nocturnally migrating prey, such as mesopelagic fish and squid (Ashmole, 1971; Imber et al., 1995; Dias et al., 2016). Furthermore, if foraging by petrels is likely to be restricted by darkness, twilight periods provide an optimal window when prey are still accessible and there is sufficient light for their visual detection.

4.4.3 Conclusions

Unlike many procellariiforms, Murphy's petrels are not directly affected by fisheries-related mortality; however, little is known about their susceptibility to variability in oceanography and climate. The amount of time that petrels spend commuting to foraging areas during incubation suggests they might be at the limit of their energetic capabilities and may be impacted by the expansion of nutrient poor areas in the South Pacific as a result of long-term increases in sea surface temperatures (Polovina et al., 2008). Whilst this study has identified important at-sea areas for Murphy's petrels that appear to vary little between years, given the huge extent of their marine ranges, site-based at-sea protection for this and other gadfly petrels would contribute rather less to their conservation than safeguarding and remediating their nesting habitats.

4.5 Abstract

The South Pacific Gyre is the world's largest expanse of oligotrophic ocean and supports communities of endemic gadfly petrels *Pterodroma* spp, yet little is known about their foraging ecology in this nutrient-poor environment. Eighteen Murphy's petrels *Pterodroma ultima* were tracked from Henderson Island, Pitcairn Islands, for two consecutive years (2011 - 2013). During pre-laying exodus, petrels travelled south and southwest of the colony, with clear sexual segregation in distribution and habitat use. During incubation, birds foraged at the southern and eastern edges of the Gyre, some taking advantage of trade winds to travel over 4,800 km from the colony, the greatest recorded foraging range of any breeding seabird. During non-breeding, the petrels migrated to the Subarctic Gyre to forage in mesotrophic waters associated with the North Pacific Transition Zone. Analysis of activity patterns indicated Murphy's petrels are amongst the most active of all seabirds, particularly during incubation when they spent c.95% of their time at sea in flight. Whilst the birds did not appear to forage at night, flight activity peaked at dawn and dusk, suggesting they feed on mesopelagic prey that are diel vertical migrants. Murphy's petrels presumably exploit nutrient-poor regions by searching large distances and taking advantage of seasonally productive frontal regions in both the North and South Pacific Oceans. At-sea protection for such a wide-ranging species would require management at huge spatial scales, and hence in the short term, the principal focus for conservation should be on eliminating the immediate threat from invasive mammals at breeding sites.

5 AGE-RELATED VARIATION IN THE FORAGING BEHAVIOUR OF AN EXTREMELY LONG-LIVED BIRD: LINKING FORAGING AND REPRODUCTIVE SENESCENCE

The data in this Chapter also appear in Clay T.A., Pearmain, E.J., McGill, R.A.R., Manica A. & Phillips R.A. Age-related variation in the foraging behaviour of an extremely long-lived bird: linking foraging and reproductive senescence. *Functional Ecology*, in review.

5.1 Introduction

Age-related variation in demographic traits is well documented in long-lived vertebrates (Jones et al., 2008; Nussey et al., 2013). Survival and reproductive performance generally increase throughout early life, stabilize during early- to mid-adulthood, and decline in old age due to senescence (Clutton-Brock, 1988; Froy et al., 2013). Identifying the selective forces shaping variation in fitness with old age is key to understanding the evolution of senescence (Nussey et al., 2013), particularly in the context of life history evolution (disposable soma theory; Kirkwood and Rose, 1991; Gaillard et al., 2010). Life history theory dictates that animals must allocate acquired energy either for somatic functions such as growth and maintenance, or for reproduction (Cody, 1966), resulting in a trade-off between investment in

current or future reproduction, and survival (Stearns, 1992). Indeed, there is empirical evidence that high allocation to reproduction or growth early in life is associated with earlier or faster senescence (Reed et al., 2008; Lemaître et al., 2015).

Studies of senescence in wild populations have tended to focus on age-related changes in fitness components; however, the focus has progressively moved towards finding changes in physiological, morphological and behavioural traits that represent the proximate drivers of senescence (Angelier et al., 2006; Lecomte et al., 2010; Nussey et al., 2011, 2013). For example, the ability to acquire energy from the surrounding environment determines the resources an individual can allocate between reproduction and self-maintenance; thus, foraging strategy is likely to play a key role in determining individual fitness (Stephens and Krebs, 1986; Forslund and Pärt, 1995; Daunt et al., 2007a). Young individuals generally have inadequate foraging skills and lack experience, and foraging performance improves during early life as they learn how and where to forage (Yoda et al., 2004; Daunt et al., 2007b). This increase in foraging efficiency is likely to be eventually offset by a decrease in muscular or physiological function (MacNulty et al., 2009), often leading to declines in foraging performance (Catry et al., 2006; MacNulty et al., 2009; Lecomte et al., 2010). There are comparatively few studies that have investigated changes in foraging parameters with old age, and in contrast with demographic traits (Nussey et al., 2013), many studies fail to find an effect (Table 5.1). Crucially, the majority of studies that find changes in foraging behaviours rarely investigate a direct link with metrics of reproductive performance or survival, without which it is not possible to draw any conclusion on whether behavioural changes have real fitness consequences. As far as I am aware, the only study to do so linked an age-related pattern in feather carbon isotope values of albatrosses in one season to a decreased probability of breeding over the following four seasons (Jaeger et al. 2014), which suggests that foraging behaviour may indeed play a key role in the ageing process.

In long-lived species, the non-breeding period represents a critical time for animals to restore body condition lost during the previous breeding season (Marra et al., 1998), yet the links between age, foraging behaviour and fitness remain largely unexplored. Indeed, there is increasing evidence that carry-over effects, i.e. events in one season that influence individual performance in a subsequent season, are important drivers of among-individual variability in fitness (Marra et al., 1998; Harrison et al., 2011). Here, I investigated age-related variation in the foraging behaviour of an extremely long-lived seabird, the wandering albatross *Diomedea*

exulans during the non-breeding period. Wandering albatross have a lifespan of 50+ years, breed biennially with a prolonged breeding season (up to a year) and experience a gradual decline in various indices of reproductive performance from 20–25 years onwards (Froy et al., 2013; Pardo et al., 2013). Studies of changes in foraging behaviour of incubating birds from the Crozet Islands have found that males, but not females forage further south with increasing age (Lecomte et al., 2010). In contrast, no age-related pattern was detected in the foraging behaviour of breeding birds from South Georgia(Froy et al., 2015), despite similar patterns of reproductive senescence (Froy et al., 2013). As far as I am aware, no studies have yet investigated foraging performance during the non-breeding season in relation to age in this or other species.

In order to test for age-related changes in distribution, diet and activity patterns in wandering albatrosses from South Georgia during the non-breeding period, serial deployments of geolocator-immersion loggers were made and feathers were sampled for stable isotope analyses. I first determined if the sample of tracked birds was sufficient to detect an age-related decline in breeding success, and subsequently tested the effect of age and sex on several indices of non-breeding foraging behaviour. In order to determine if age-related changes in foraging behaviour had an effect on fitness, I linked foraging behaviours that showed variation with age to breeding success in the following season. I hypothesized that senescence in foraging behaviour would be detectable during the non-breeding season, as individuals that do not acquire sufficient resources for somatic maintenance, including feather moult (Prince et al., 1997), would be in poorer condition in the subsequent breeding season. Indeed, it might be expected that older birds would differ from young or middle-aged individuals in their activity at particular times of the year, related to periods of energetic constraint. To that end, I investigated whether there was seasonal variation in the activity patterns of wandering albatrosses that covaried with age.

In many migratory animals, such as seabirds, winter activity has been shown to have a carry-over effect on breeding performance in the subsequent breeding season (e.g. Daunt et al. 2014, Shoji et al. 2015). However, carry-over effects might present themselves only at particular ages, such as in older birds, as a consequence of physiological impairment. In order to incorporate the effect of age on the relationship between foraging behaviour and breeding success with age, I included the interaction between age and metrics of foraging behaviour when looking at drivers of variation in breeding success. Specifically, I expected that old

birds would 1) have reduced activity, and forage further south thanyounger birds, based on results of previous studies during breeding (Table 5.1; Catry et al., 2006, 2011b; Lecomte et al., 2010), 2) would have a lower probability of breeding successfully in the following season, and 3) that a reduction in activity and a more southerly distribution with increasing age would be linked to lower breeding success.

5.2 Methods

5.2.1 Study site and data collection

Fieldwork was carried out at a long-term wandering albatross study colony on Bird Island, South Georgia (54°00' S, 38°03' W). Chicks have been ringed annually since 1972 and the majority of the population is of known age. Birds of unknown age were assigned a conservative minimum age of 7 years when first ringed as breeding adults (Weimerskirch, 1992). Regular monitoring of nests has been conducted since 1980 and breeding success is determined from daily visits during the laying, hatching and fledging periods, and weekly visits at other times. Geolocator-immersion loggers (MK3-5 and MK7, 3.5–9 g; BAS, Cambridge, UK) were deployed on the tarsus of breeding adults between February 2004 and January 2009 and retrieved between November 2008 and January 2011, as part of a long-term tracking program. The data included below correspond to two consecutive non-breeding periods (2008 and 2009) and their subsequent breeding seasons (2009 and 2010). Body feathers for stable isotope analyses were collected from a subset of individuals at device retrieval, and some loggers failed to record immersion data, thus sample sizes vary (Table A4.1). Birds were sexed from field observations (size and plumage dimorphism, copulatory position) or using molecular methods (Froy et al. 2013).

5.2.2 Data processing

Light data were processed using the BASTrak software suite (BAS, Cambridge, UK) providing two positions per day with a mean error of 186 ± 114 km (Phillips et al., 2004b). Locations with interruptions around sunrise and sunset and periods around the equinox (3 to 4 weeks) were excluded, when latitude cannot be estimated reliably. Loggers tested for saltwater immersion every 3 s, storing the sum of positive tests at the end of each 10 min period, providing a value ranging from 0 (continuously dry) to 200 (continuously wet). For

each individual, the non-breeding period was defined as the time from the start of outward migration to return to breeding grounds, and was derived from location and immersion data. Take-offs and landings are energetically expensive in wandering albatrosses (Weimerskirch et al., 2000a; Shaffer et al., 2001a) and most prey are detected in flight and caught just after landing (Weimerskirch et al., 1997). Consequently, the following activity metrics were chosen to represent foraging effort: the proportion of time spent in flight (proportion of time spent dry), the duration of flight (dry) bouts in minutes and the number of landings (wet bouts) per hour. Loggers did not record the exact number of landings in a given 10 min interval, so these indices used here should be considered as minimum values (see Appendix 4 for further details).

Stable isotope analysis was carried out on three body feathers per individual, providing information on carbon source (i.e. foraging habitat, $\delta^{13}C$) and trophic level ($\delta^{15}N$) of prey at the time of feather moult (Phillips et al., 2009a). As wandering albatrosses gradually replace their plumage at the non-breeding grounds (Prince et al., 1997; Battam et al., 2010), multiple feathers were analysed to better represent possible shifts in habitat during this period (Jaeger et al., 2009). Feathers were prepared following standard procedures and stable isotope ratios were determined by continuous flow mass spectrometry (see Appendix 4 for details).

5.2.3 Data analysis

5.2.3.1 Age-related variation in fitness and behaviour

Analyses of age-related variation were carried out using linear models (LM) for normally distributed data and generalized linear models (GLM) for binomial distributions. I first tested the relationship between age and arrival date at the breeding colony, and in subsequent breeding parameters (probability of breeding, the date of laying and breeding success, and the relationships between these variables). Analyses were conducted separately for the full sample of tracked birds, and for the reduced sample with immersion data, and the relationships with breeding success examined for all monitored individuals (see Appendix 4 for details). I investigated age-related variation in stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$), spatial metrics (latitude, longitude, distance travelled per day, distance from the colony, the sizes [areas] of core [50% utilization distributions, UD] and general home ranges [95% UD]) and activity patterns (number of landings per hour, average flight bout durations and time spent in flight). In order to investigate if latitude and $\delta^{13}C$ were linked in this study (Jaeger et

al. 2010), I calculated the Pearson's correlation between the median latitude and the average of δ^{13}C values of each bird. I also mapped the distribution of birds with the highest (> -17 ‰) and lowest (< -19 ‰) average values of δ^{13}C to visualize the isotopic landscape in geographic space (See Appendix 4).

Activity variables were calculated for daylight and darkness periods separately, as albatross activity patterns vary according to photoperiod (Phalan et al., 2007). The median value of each spatial and activity metric was computed for each individual. Models for δ^{13}C and δ^{15}N were run with bird identity as a random effect within the R package *lme4* (Bates et al., 2015), as there were multiple values per individual. Each metric was included as a response variable in a standalone model with age, sex, tracking year, previous breeding outcome (success or incubation failure) and the interaction between age and sex to control for sex-specific differences with age (Lecomte et al., 2010), as predictors. Distance from the colony and area of the core and general home range variables were log transformed to improve data spread. All possible models were ranked according to Akaike Information Criterion (AIC) values where the best model was the one with the lowest AIC value (Burnham and Anderson 2002). If multiple models were within 2 AIC units of the best-supported model, the most parsimonious model (with fewer parameters) was chosen (Burnham and Anderson 2004, Arnold 2010).

In order to investigate if there was seasonal (monthly) variation in activity patterns across the non-breeding period of birds, and whether this varied with age, I tested the effect of month and age-class on the number of landings and time spent in flight (see Appendix 4). Additionally, I used a randomization procedure to test whether albatrosses differed in their spatial distributions by age, sex and year of tracking (Clay et al., 2016). See Appendix 4 for further details.

5.2.3.2 Linking age-related variation behaviour with fitness

I investigated the link between non-breeding behaviour and subsequent breeding outcome, only considering variables for which there was a significant change with age. I hypothesized that birds that defer breeding or fail during early breeding were in poorer condition on return to the colony than birds that went on to breed successfully (Weimerskirch, 1992). The response variable was the probability of successful breeding (1 = chick fledged and 0 = egg failure or breeding deferral; the single individual that failed in chick-rearing was excluded as

this was more likely to reflect factors other than body condition at return) and GLMs were run for each behaviour separately, due to differences in sample sizes between datasets (Table A4.1). I tested four potential scenarios: 1) the behaviour of interest is the driver of reproductive senescence (the behavioural variable explains as much or more variance in reproductive success than age). There might also be variation in behaviour that influences fitness only at particular ages; either, 2) birds would decrease their activity with age, and lower activity would lead to reduced fitness (the link between behaviour and fitness is stronger with age), or 3) lower activity would result in increased fitness (suggesting evidence of increased experience with age and not foraging senescence). Finally, 4) there might be no link between the behaviour and fitness. In order to test the first scenario, models were run with just the behavioural variable as a predictor (as a proxy for age), and in order to test scenarios 2–4, the behaviour variable, age and the interaction between age and the behaviour variable were included as fixed effects. Where previously a significant effect of sex on that behaviour was found, the interaction with sex was also included. All analyses were conducted in R v. 3.3.1 (R Core Team, 2014). Unless otherwise reported, data are presented as a mean ± standard error (SE).

Table 5.1. Summary of studies that investigate changes in foraging behaviour of wild populations with old age.

Species	Site	Season	Behaviour and statistical significance	Relationship	Sex-specific	Reference
Vertebrates – Birds						
Audouin's gull Larus audouinii	Ebro Delta	Br (I)	Diet (from δ13C and δ15N) (↑ and ↓)	Linear	NT	Navarro et al. 2010
Cory's shearwater Calonectris borealis	Selvagens Is.	Br (I)	No. landings daylight (×) and darkness (↓), time on water (×), trip duration (×)	Factor (26+)	Both	Catry et al. 2011
Grey-headed albatross Thalassarche chrysostoma	South Georgia Is.	Br (I)	Trip duration (↑), daily mass gain (↓)	Factor (35+)	♂	Catry et al. 2006
King penguin Aptenodytes patagonicus	Crozet Is.	Br (CR)	Dive depth (×), duration (×), dynamic body acceleration (↓).	Factor (8+)	Both	Le Vaillant et al. 2012,
			Dive depth (↑), δ15N (↑), trip duration (↓), prey pursuits (↑)		♀	2013
			Mass gain (↑), δ13C (×),		Both	
Little penguin Eudyptula minor	Phillip Is.	Br (CR)	Dive duration (↑), dive effort (↑)¥, foraging area (↓), distance from shore (↓), dive depth (×), δ13C (×), δ15N (×)	Factor (11+)	Both	Zimmer et al. 2011; Pelletier et al. 2014
Brünnich's guillemot Uria lomvia	Coats Is.	Br (CR)	Dive depth (×), shape (×) and surface interval (×)	n/a	Both	Elliott et al. 2015

Wandering albatross Diomedea exulans	Crozet Is.	Br (I)	Foraging latitude (↓) and range (↑), trip duration (×), distance travelled (↑), δ13C (↓), δ15N (×), time on water (×) and in flight (↑)	Linear	♂	Lecomte et al. 2010; Jaeger et al. 2014
		NB	δ13C (↓), δ15N (↓)	Linear	Both	Jaeger et al. 2014
	South Georgia Is.	Br (I + CR)	Foraging latitude (×), trip duration (×), distance travelled (×), no. landings (×), time on water (×)	n/a	Both	Froy et al. 2015
Vertebrates – Mammals						
Bottlenose dolphin Tursiops cf. aduncus	Shark Bay	BR	Time acquiring (×), travelling (×) and foraging with tool (×)	n/a	♀ (♂ NT)	Patterson, Krzyszczyk & Mann 2015
Grey-wolf Canis lupus	Yellowstone	BR	Predatory performance (↓)	Quadratic	Both	MacNulty et al. 2009.
Moose Alces alces	Isle Royale	Winter	Distance from shore (↓)	Factor (10+)	Both	Montgomery et al. 2013, 2014
Northern elephant seal Mirounga angustirostris	Año Nuevo	Post-breeding	Foraging time (×), distance* (×), dive structure (×)	n/a	♀ (♂ NT)	Hassrick, Crocker & Costa 2013
		Post-moult	Foraging time (×), distance* (×), dive structure (✓)	Linear	♀ (♂ NT)	
Soay sheep Ovis aries	St Kilda Is.	Year-round	Home range size (♂=↑ & ♀=↓) and quality (♂=↑ & ♀=↓)	Nonlinear	♀ cf. ♂	Hayward et al. 2015
Southern elephant seal Mirounga leonina	Kerguelen Is.	Year-round	δ13C (↓)	Linear	Both	Authier et al. 2012
Invertebrates						
Honeybee Apis mellifera	Algonquin Park	NA	Rate of food delivery (↓) Trip duration (↑)	Quadratic Linear	♀	Dukas 2008

Br = Breeding, NB = non-breeding, I = incubation, CR = chick-rearing. Where there are statistically significant changes with age, the direction is given (into older age): ↑ = increase, ↓ = decrease. ✓ *and* ✗ *indicate statistically significant changes where the direction is not given, and non-significant changes, respectively. Factor = age class categorical variable (with the oldest age category indicated in parentheses), Linear, nonlinear or quadratic = relationships with age included as a continuous variable, n/a = not applicable.* ♂ *= only significant in males and* ♀ *= in females, NT = sex differences not tested,* ♀ *cf.* ♂ *= different results in males and* females, Both = similar results in males and females No. = number, *Foraging time, distance and dive structure = principal component of behavioural variables, [¥]dive effort = index of relationship between dive duration and post-dive duration. For non-linear relationships, direction of effect is indicated from middle to old age.

5.3 Results

5.3.1 Age-related variation in fitness

The non-breeding migrations of 82 adults were tracked with geolocators, and immersion or stable isotope data were obtained for 49 and 48 individuals, respectively (Table A4.1). There was a significant relationship between age and subsequent breeding success, in both the full sample of tracked birds (n = 73, ΔAIC = -6.97, χ_1^2 = 9.20, P = 0.002) and the reduced sample with immersion data (Fig. 1; n = 42, ΔAIC = -7.31, χ_1^2 = 9.63, P = 0.002), with individuals more likely to fail aged 20 years onwards (Fig. 5.1a, Table 5.2). At the population-level, there was a quadratic relationship with age, with lower breeding success in young (<15 years) and old birds (30+ years) (Fig. 5.2, Table A4.2). There was no interaction between age and sex in the sample of tracked birds (Table 5.2). Breeding success of tracked birds was significantly higher in 2009 (0.95 ± 0.03) than in 2010 (0.74 ± 0.08) (Table 5.2), reflecting annual differences at the population-level (overall colony breeding success ± SE in 2009: 0.81 ± 0.01, and 2010: 0.73 ± 0.02), and was higher for previously successful breeders (0.89 ± 0.04) than birds that failed during incubation the previous season (0.75 ± 0.16) (Table 5.2). A greater proportion of tracked birds attempted to breed in 2009 (1.00 ± 0.00) than in 2010 (0.78 ± 0.07) (Table 5.2), reflecting annual differences at the population-level (probability ± SE in 2009: 0.62 ± 0.02, and 2010: 0.55 ± 0.02). Females arrived at the breeding colony significantly later than males (Table 5.2; mean ± SD: 1 December ± 8 days and 26 November ± 5 days, respectively), but there were no significant effects of age, sex, year and breeding status on laying dates. There was no effect of arrival date on breeding probability (ΔAIC = 1.46, χ_1^2 = 0.65, P = 0.42), laying date (ΔAIC = 1.04, χ_1^2 = 42.87, P = 0.24) or breeding success (ΔAIC = 1.92, χ_1^2 = 0.20, P = 0.65), nor of laying date on breeding success (ΔAIC = 2.25, χ_1^2 = <0.01, P = 0.98).

Table 5.2. Summary of the most parsimonious models explaining variation in the arrival date at the colony and in the subsequent breeding parameters for non-breeding wandering albatrosses.

Response	N	Predictor variables					ΔAIC
		Age	Sex	Age:Sex	Year	Status	
Breeding success	73	X	–	–	X	X	0.00
Lay date	32	–	–	–	–	–	0.00
Breeding probability	82	–	–	–	X	–	0.42
Arrival date	69	–	X	–	–	–	0.00

Status = a factor denoting previous breeding outcome; N = number of individuals; X = predictor variables retained; – = predictor variables not retained in the most parsimonious models; ΔAICc = change in Akaike information criterion, corrected for small sample sizes, from most parsimonious model

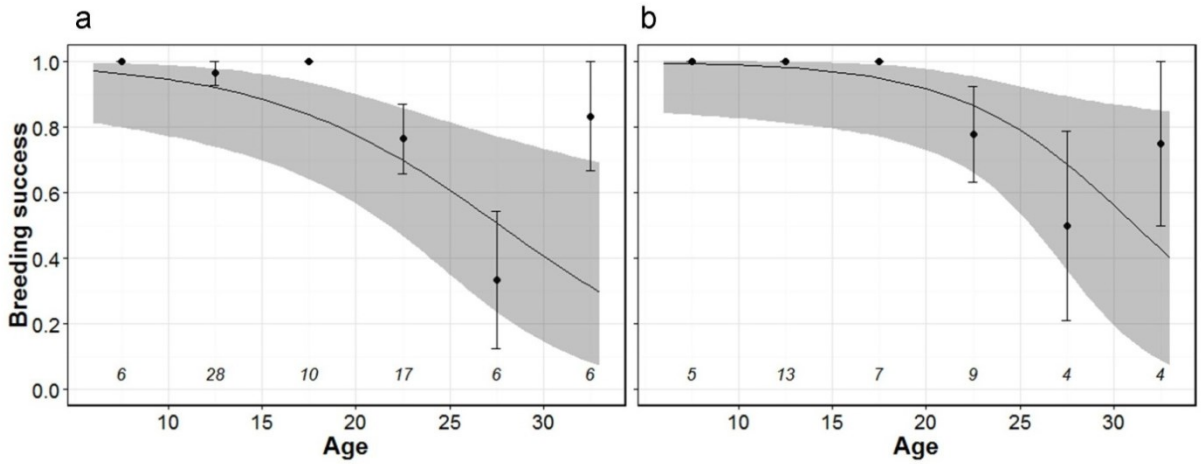


Figure 5.1. Relationship between age and subsequent breeding success for non-breeding wandering albatrosses tracked with geolocators from Bird Island, for: a) all birds tracked (*n* = 82) and b) birds with immersion data (*n* = 46). The modelled relationship of age is shown by a solid black line with SE as a shaded grey polygon. The mean ± SE breeding success is shown for each five-year age bins along with the sample size.

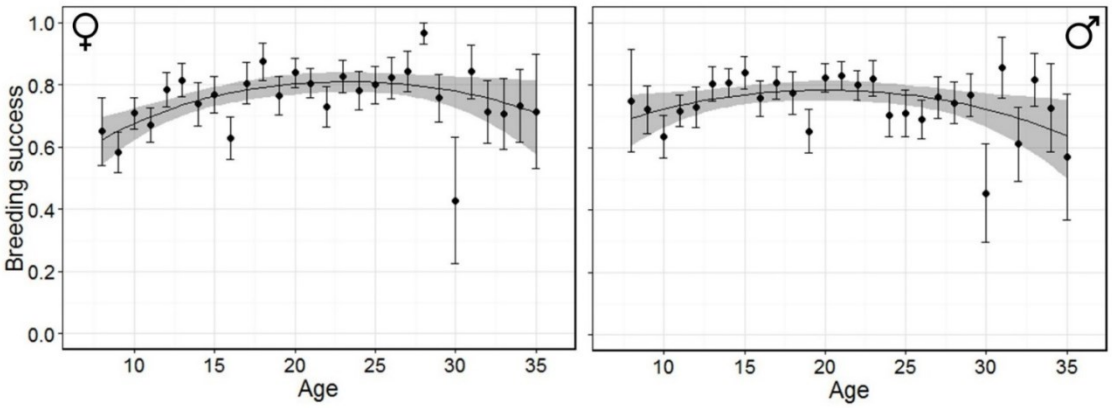


Figure 5.2. Relationship between age and breeding success for all monitored female (♀, *n* = 1,139) and male (♂, *n* = 1,204) wandering albatrosses at Bird Island in the 2009 and 2010 breeding seasons (pooled). Points show the mean proportion that bred successfully for each age ± SE. The quadratic relationship with age best predicted breeding success of both sexes and is shown by the solid line, with shaded grey polygons representing the SE around modelled predictions.

5.3.2 Age-related variation in foraging behaviour

The tracked birds dispersed across the Southern Ocean with core areas mainly in the southwest Atlantic and southeast Pacific Oceans: around the Patagonian Shelf break, in the Drake Passage and in the Humboldt Current off the coast of southern Chile (Fig. 5.3). They also foraged to a lesser extent around the Prince Edward Islands in the southwest Indian Ocean and around the Chatham Rise, east of New Zealand. There was no evidence of spatial segregation by age class for males and females pooled (Fig. 5.3, Table 5.3), or when tested separately (Table A4.4); however, males and females were more spatially segregated than expected by chance (Fig. A4.1, Table 5.3). Sex differences in distributions were linked to both longitude and latitude (Fig. 5.4c, d). Females migrated further east than males and so were more likely to use the Indian Ocean, whereas males were more likely to use the Pacific Ocean (Fig. A4.1); however, there was no difference in the median distance from the colony of males and females (Table 5.4). Females used waters on average 2.8° further north (Fig. 5.4c), and sexual segregation of core areas appeared to be driven predominantly by latitudinal differences (Fig. A4.1). Males used a region in the southern Humboldt Current and the Drake Passage, whereas females were more likely to use the Patagonian Shelf and the Brazil-Falklands Confluence. In both sexes there was a linear decrease in latitude but not longitude

with age (Table 5.4, Fig. 5c; modelled change of -2.5° from 9–33 years). There were no differences in any other spatial metric with age or sex (Table 5.4).

Table 5.3. Observed and randomized spatial overlap (Bhattacharyya's affinity, BA) of core (50%) and general use (95%) utilization distributions (UDs) of wandering albatrosses, compared between age classes, sex and tracking year.

	50%			95%		
Class	Observed	Randomized	*P*	Observed	Randomized	*P*
Age (both sexes)	–	–	–	–	–	–
Y vs. M	0.45	0.43 ± 0.03	0.95	0.86	0.87 ± 0.02	0.14
M vs. O	0.44	0.42 ± 0.03	0.91	0.85	0.85 ± 0.03	0.53
Y vs. O	0.42	0.40 ± 0.04	0.79	0.84	0.84 ± 0.03	0.46
Sex (all ages)	0.38	0.44 ± 0.02	**0.002**	0.81	0.89 ± 0.02	**<0.001**
Year	0.42	0.44 ± 0.02	0.13	0.87	0.89 ± 0.01	0.14

Y = young (6–14 years); M = middle-aged (14–24 years); O = old (25+ years). Randomized overlaps are shown as a median ± interquartile range. P represents the proportion of randomized overlaps that were smaller than the observed.

Despite large variability in $\delta^{13}C$, values were lower in males than females (by -0.5 ‰) and both sexes exhibited a significant age-related decline (Table 5.4, Fig. 5.4a; modelled change of -0.7 ‰ from 9–33 years). However, there was no correlation between the average $\delta^{13}C$ values and median latitude of each bird (Pearson's product-moment correlation = 0.27, *df* = 47, t = 1.89, *P* = 0.06). In order to determine the links between $\delta^{13}C$ and spatial distribution, I mapped the distributions of individuals with the highest (> -17 ‰) and lowest (< -19 ‰) average values of $\delta^{13}C$ (Fig. A4.3). Birds with high $\delta^{13}C$ values appeared to use more northerly waters (around the Subtropical Front) and forage closer to the coast (within the 1,000 m isobath). In contrast, birds with low $\delta^{13}C$ values appeared to forage further south in association with the Polar Front, and in deeper, pelagic waters (Fig A4.4). The large proportion of variance explained by the random effect of individual identity indicates that

feather isotope ratios were individually repeatable (Table 5.4). There were no differences in $\delta^{15}N$ with age or sex (Table 5.4).

There was a significant linear decrease in the number of landings during daylight with age for both males and females (modelled change of -0.04 landings hr^{-1} [11%]), but no effect of age on the other five metrics (Fig. 5.4, Table 5.4). Males landed less often than females during darkness (by 0.02 landings hr^{-1}) and spent less time in flight during daylight (by 28 min day^{-1}) (Fig. 5.4e). There was a significant change in activity patterns across the non-breeding period, best explained by a cubic relationship with month (Table A4.5). Over the first three months, birds almost halved the rate of landings and time spent flying, and from February–May, exhibited much lower activity (Fig. 5.5). Birds increased their flight and foraging activity in June, peaking in the three months before returning to the colony. Although old birds (25+ years) appeared to be less active in the last three months before return to the colony (Fig. 5.5), age class was not significant (Table A4.5). There was no effect of the interaction between age and sex, year or status on any of the metrics of foraging behaviour during the non-breeding season (Table 5.4), nor was there evidence of spatial segregation between years (Table 5.3).

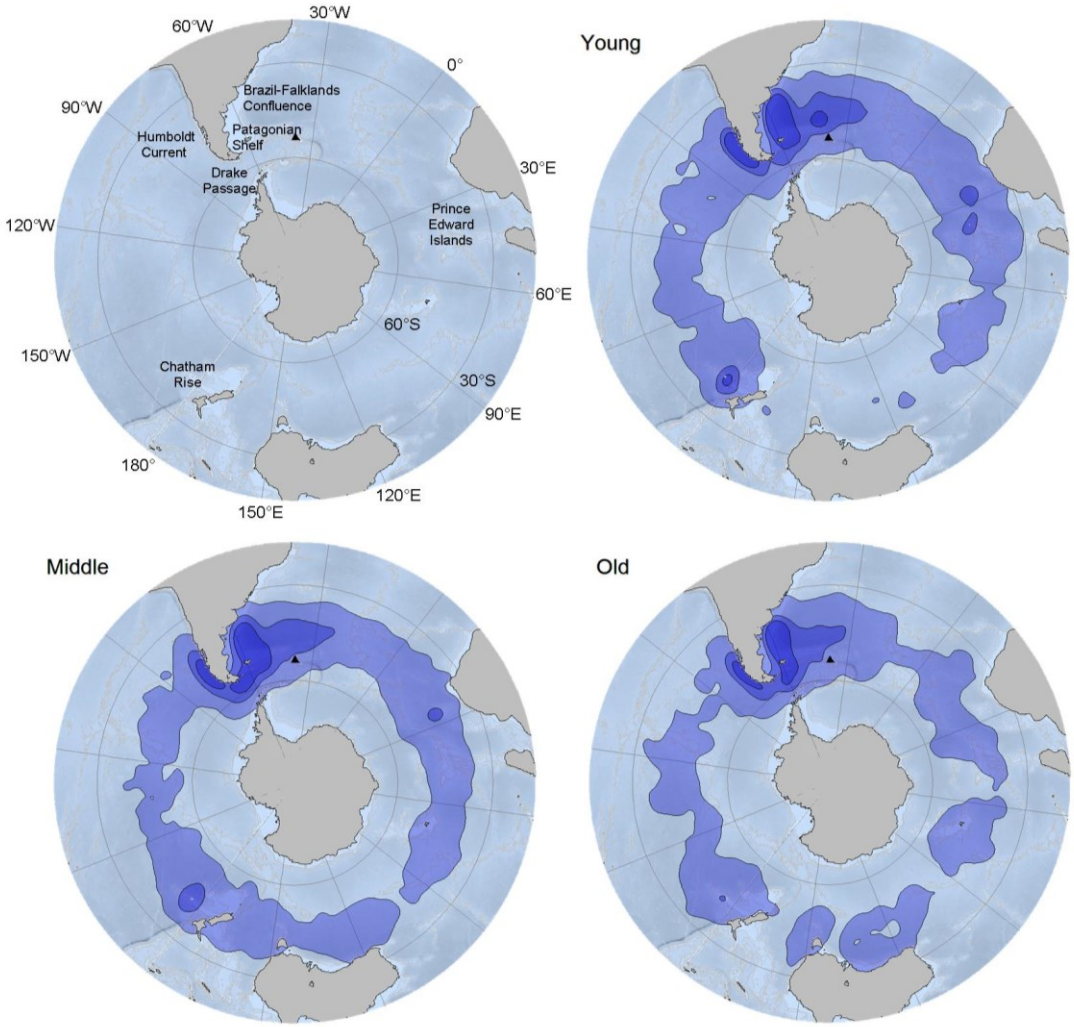


Figure 5.3. Map of study region and core (25% and 50%) and general use (95%) utilization distributions (UDs) of young (6–14 years, n = 27), middle-aged (15–24 years, n = 29) and old (25+ years, n = 17) wandering albatrosses tracked with geolocators from Bird Island (black triangle) during non-breeding.

Table 5.4. **Summary of the best models explaining variation in the foraging behaviour of non-breeding wandering albatrosses.**

Category	Response variable	*N*	Predictor variables					ΔAICc	R^2 marginal	R^2 conditional
			Age	Sex	Age: Sex	Year	Status			
Moulting habitats	δ^{13}C (‰)	48	X	X	–	–	–	1.04	0.09	0.49
	δ^{15}N (‰)		–	–	–	–	–	1.84	–	0.24
Space use	Latitude (°)	82	X	X	–	–	–	0.00	0.24	–
	Longitude (°)		–	X	–	–	–	0.93	0.06	–
	Distance travelled day^{-1} (km)		–	–	–	–	–	0.70	–	–
	Distance to colony (km)		–	–	–	–	–	0.00	–	–
	Area of 50% UD (km^2)		–	–	–	–	–	0.17	–	–
	Area of 95% UD (km^2)		–	–	–	–	–	0.00	–	–
Activity patterns	No. landings hr^{-1} light	49	X	–	–	–	–	0.00	0.05	–
	No. landings hr^{-1}dark		–	X	–	–	–	0.00	0.08	–
	Flight bout length light (hrs)		–	–	–	–	–	0.00	–	–
	Flight bout length dark (hrs)		–	–	–	–	–	0.00	–	–
	Time in flight light (hrs)		–	X	–	–	–	0.00	0.05	–
	Time in flight dark (hrs)		–	–	–	–	–	0.00	–	–

All are linear models (LM) except for $\delta^{13}C$ and $\delta^{15}N$, where multiple values were used per individual, and so bird identity was included as a random effect. $R^2_{marginal}$ = the proportion of variance by the fixed effects, and $R^2_{conditional}$ = fixed plus random effects .

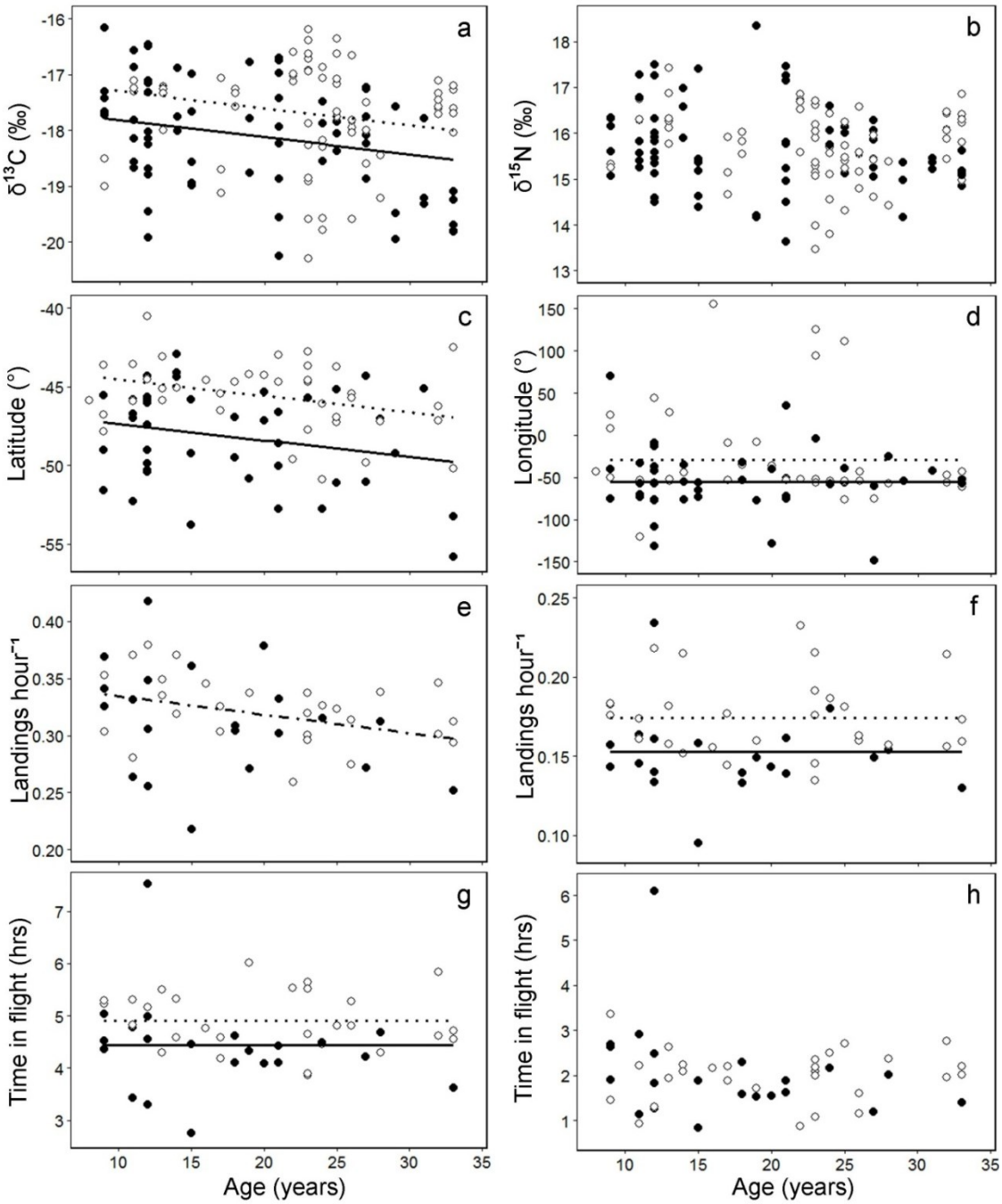


Figure 5.4. Relationship between age and non-breeding foraging behaviour for male (filled circles) and female (closed circles) wandering albatrosses tracked with geolocators from Bird Island. Variables shown are a) δ13C and b) δ15N values in body feathers, and median values for c) latitude, d) longitude, e) number of landings per hour during daylight and f) darkness, and g) number of hours spent in flight during daylight and h) darkness. Age was modelled as a linear variable. Where a significant effect of sex was found, males (solid) and females (dotted) are shown with separate lines; where it

was not, both sexes are shown with the same line (dotdash). Horizontal lines indicate no age effect but a significant sex effect.

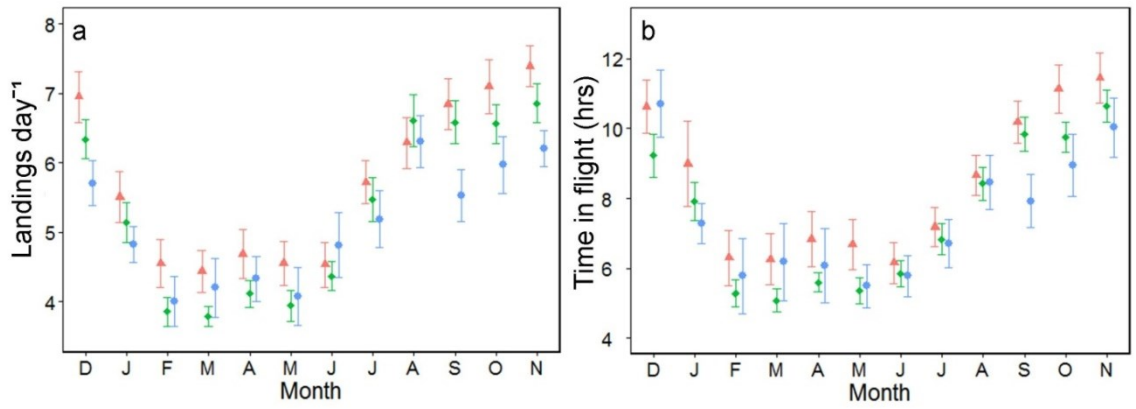


Figure 5.5. Monthly variation in the a) number of landings per day and b) time spent flying per day of young (red triangles, 6–14 years), middle-aged (green diamonds, 15–24 years) and old (blue circles, 25+ years) non-breeding wandering albatrosses tracked with geolocators from Bird Island. Values are mean ± SE of individual monthly medians for light and dark periods combined.

5.3.3 Linking age-related variation in foraging behaviour with fitness

I investigated the relationship between the three behavioural metrics that showed a linear decrease with age (δ^{13}C, latitude and number of landings during daylight) and the probability of successful breeding in the following season. When included as a standalone variable, there was no effect of any of the three behavioural metric on subsequent fitness (δ^{13}C: n = 45, ΔAIC = 2.07, χ^2_1 = 0.03, P = 0.87; latitude: n = 78, ΔAIC = 1.73, χ^2_1 = 0.37, P = 0.54; landings: n = 48, ΔAIC = 1.62, χ^2_1 = 0.55, P = 0.46). With the inclusion of the age interaction, there was a significant effect of the number of landings (but not the other variables) on the probability of successful breeding in the following season (Table 5.5). Breaking down this interaction revealed that all birds younger than 20 years old bred successfully the following season; however, older birds (20+ years) with higher landing rates were more likely to defer breeding or fail during incubation (0.33 ± 0.01 landings hour^{-1}) than older birds with lower landing rates (0.30 ± 0.01 landings hour^{-1}) (Fig. 5.6).

Table 5.5. Summary of the top five models linking age-related variation in foraging variables of non-breeding wandering albatrosses with reproductive performance in the following season (1 = chick fledged, 0 = failed in incubation or deferred breeding).

Variable	Age	Variable: Age	Sex	Variable: Sex	AICc	ΔAICc	Weight
No. landings hr^{-1} light							
X	**X**	**X**	**n/a**	**n/a**	**33.0**	**0.0**	**0.81**
X	X	–	n/a	n/a	36.3	3.3	0.16
–	X	–	n/a	n/a	40.1	7.1	0.02
–	–	–	n/a	n/a	45.3	12.3	<0.01
X	–	–	n/a	n/a	47.0	13.9	<0.01
Latitude (°)							
–	**X**	–	–	–	**75.5**	**0.0**	**0.34**
X	X	–	–	–	77.6	2.1	0.12
–	X	–	X	–	77.6	2.2	0.12
X	X	–	X	–	77.9	2.4	0.10
–		–	–	X	78.4	3.0	0.08
δ^{13}C (‰)							
–	–	–	–	–	**36.1**	**0.0**	**0.38**
–	X	–	–	–	38.1	2.0	0.14
–	–	–	X	–	38.1	2.0	0.14
X	–	–	–	–	38.1	2.1	0.14
X	X	–	–	–	40.1	4.1	0.05

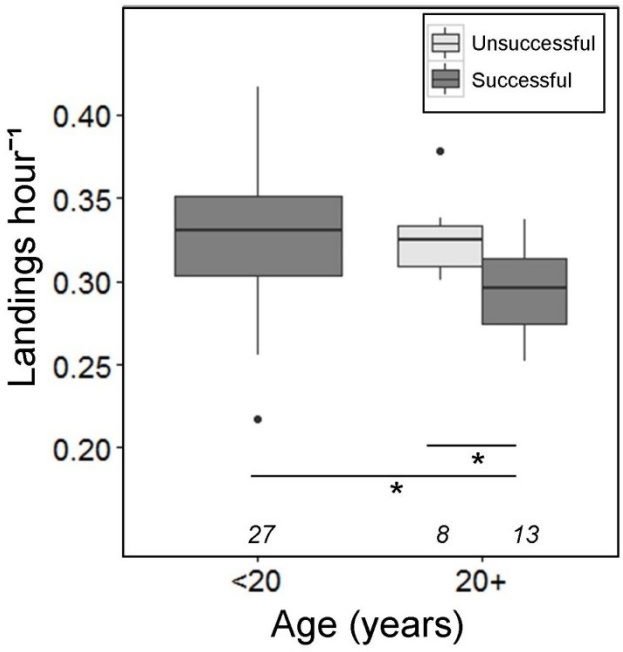


Figure 5.6. The interaction between age and the number of landings per hour in daylight during non-breeding on subsequent reproductive performance for wandering albatrosses tracked with geolocators from Bird Island. Successful = chick fledged; Unsuccessful = failed in incubation or deferred breeding. For illustrative purposes, age is split into two categories as all birds younger than 20 years old bred successfully the following season. The number of individuals for each category is given at the bottom of the plot. * P < 0.05

5.4 Discussion

There is limited evidence of changes in the foraging behaviour of wild animals with old age (reviewed in Table 5.1) and the links between particular foraging strategies and age-related declines in fitness remain poorly characterised. Indeed, while there are a growing number of studies that link changes in winter foraging behaviour to subsequent breeding success (Daunt et al. 2006, 2014, Shoji et al. 2015, Fayet et al. 2016), as far as I am aware, this is the first study to demonstrate an age-specific carry-over effect of non-breeding foraging behaviour. In the following sections, I discuss these results and their implications for the study of senescence in long-lived species.

5.4.1 Age-related variation in foraging behaviour

In this study, I find that with increasing age, both non-breeding male and female wandering albatrosses are distributed further south, have lower $\delta^{13}C$ values and make fewer landings. Previous studies of birds from the Crozet Islands revealed an unexpected foraging pattern with age, in that older males foraged south of the Polar Front during incubation, leading to spatial segregation from females that remained in subantarctic and subtropical waters (Lecomte et al., 2010). Although this pattern was not found in birds from South Georgia during breeding (Froy et al., 2015), these results corroborate the inference from $\delta^{13}C$ values that older birds are distributed further south outside the breeding period (Jaeger et al., 2014). Accordingly, there was a decrease in both the average latitude, and $\delta^{13}C$ of body feathers with age, but no correlation between the two. The latter supports a recent study which concluded there was no clear latitudinal gradient in $\delta^{13}C$ values in the southwest Atlantic Ocean because the horizontal stratification of water masses shows less spatial structure than in the Indian Ocean (Ceia et al., 2015).

It has been hypothesized that old males forage further south either as a result of competitive exclusion by younger birds, or to take advantage of stronger winds, thereby reducing flight costs (Lecomte et al., 2010; Jaeger et al., 2014). Competitive exclusion during non-breeding appears unlikely, as there is no evidence of spatial segregation during breeding when competition is presumed to be much higher (Froy et al., 2015). It appears more likely that old birds would reduce foraging costs by using more favourable winds further south (Weimerskirch et al., 2000a); however, unlike at Crozet (Lecomte et al., 2010; Jaeger et al., 2014), there were no negative demographic consequences of a shift in distribution with age. This may be due to differences in wind regimes and in the availability and productivity of habitats in the two regions (Phillips et al., 2009b). While I found no evidence of spatial segregation between age classes, there was some segregation of males and females. Sexual segregation is well documented in breeding seabirds, particularly those with large sexual size dimorphism, but there is less evidence during the non-breeding season (Phillips et al., 2011). Male wandering albatrosses are 20% larger than females (Shaffer et al., 2001b), and their higher wing loading makes them more efficient at foraging further south than females in windier latitudes (Weimerskirch et al., 1993; Shaffer et al., 2001b). This pattern appears to persist during non-breeding, as documented elsewhere (Jaeger et al., 2014; Chapter 3; Clay et al., 2016), with females from South Georgia less likely to forage in the Drake Passage and

Humboldt Current than males and more likely to forage off the Patagonian Shelf up to the Brazil-Falklands Confluence. Wandering albatrosses are caught as bycatch in pelagic longline fisheries in the southwest Atlantic Ocean and the lower survival of females compared with males (Croxall et al., 1990; BAS, unpublished data) has been attributed to sex differences in bycatch as a result of greater overlap of females than males with fishing vessels during breeding (Jiménez et al., 2016). I emphasize that females may also be at much greater risk than males during the non-breeding season, a period representing a considerable portion of their adult lives.

Most foraging activity of albatrosses takes places during daylight (Phalan et al., 2007), and take-offs and landings are the most energetically costly behaviours (Shaffer et al., 2001a). The number of landings in this study is likely to be underestimated by the low resolution of the activity loggers; regardless, the 11% decrease in landings per hour during daylight from youngest to oldest birds, represents a notable change in foraging effort. Albatrosses have lower energy requirements during the non-breeding period, but have to undergo a partial moult of flight feathers which will reduce flight and foraging efficiency (Prince et al., 1997; Weimerskirch et al., 2005). As such, birds probably target predictable and seasonally abundant food resources to reduce movement costs (Battam et al., 2010). There was a notable reduction in activity from February to May, which is probably associated with flight feather moult (Cherel et al., 2016), rather than a change in habitat use. In albatrosses, the duration of the non-breeding period is the main constraint on the degree of moult, and wandering albatrosses that fail do not have as much time to renew as many feathers if they are to breed in the following season, as do successful birds that take a year off (Prince et al., 1997). This period of lower activity represents only half of the non-breeding season, and subsequently, activity increases markedly in the months before breeding. This confirms that feather moult may be a major driver of time budgets during non-breeding, with potential consequences for fitness.

5.4.2 Links with fitness: foraging senescence or experience with age?

Old animals are expected to suffer from deterioration in muscular or physiological condition (Nussey et al., 2013), which is reflected in reduced foraging activity or ability (Catry et al., 2006; MacNulty et al., 2009). However, reduced activity may not necessarily indicate a decrease in foraging success (i.e. foraging senescence), if animals are able to increase their

foraging efficiency with age (Weimerskirch et al., 2005; Catry et al., 2011b). As predicted, older birds were less active than younger birds; however, in contrast to my prediction that less active individuals would have a lower probability of breeding successfully, reduced foraging activity of older birds was linked to higher fitness. I therefore infer that reduced activity is not a direct indication of poor foraging ability, but that birds able to reduce their foraging effort are probably more efficient. Whether this trend results from selective mortality of poor foragers or from individual improvements with age is not clear in this study, and is discussed below.

There is increasing evidence that non-breeding behaviour influences subsequent breeding outcome, particularly in seabirds, where increased activity has been linked to higher subsequent reproductive effort (Fayet et al., 2016a), or to decreased probability of breeding, later laying and lower breeding success the following season (Daunt et al., 2006; 2014; Shoji et al., 2015). These studies suggest that individuals may compensate for poor condition by increasing their foraging effort, but with repercussions for reproductive performance in the following season. Indeed, wandering albatrosses with lower mass on return to the breeding colony are less likely to breed (Weimerskirch, 1992). In this study, the few birds that deferred breeding or bred unsuccessfully were all 20+ years old. The large individual variability in foraging effort of young and middle-aged birds suggests that there is little direct cost, in terms of fitness, of high foraging activity. In contrast, older individuals with higher foraging activity appeared to pay a price for greater effort. As this study included young individuals with low foraging activity, but lacked old birds with high foraging activity, it is likely that, over the course of their lives, birds with consistently high effort are selected against (Daunt et al., 2007a; Fay et al., 2016). Similarly, I speculate that if individuals are in poor condition, it may be optimal to increase effort allocated to self-maintenance at the risk of breeding failure (McNamara et al., 2009), supported by evidence that breeding albatrosses maintain a high level of physiological fitness into old age (Lecomte et al., 2010); however, this would need to be confirmed by data on physiology, condition and foraging success of non-breeders. As suggested by a recent conceptual study, the inability of animals to recover body condition between breeding attempts may an important driver of senescence (Senner et al., 2015), potentially mediated through foraging ability.

As this study is cross-sectional, the observed patterns in behaviour could have arisen through two principal mechanisms; within-individual increases in foraging experience or selective

mortality of particular phenotypes (Forslund and Pärt, 1995). Young birds have to reach a threshold mass to be able to recruit into the breeding population, and the improvement in foraging efficiency is likely to be an important determinant of breeding success in early life (Weimerskirch, 1992; Froy et al., 2013). While increased foraging experience in old age is poorly documented (but see Zimmer et al., 2011; Vaillant et al., 2013), it has been suggested that where changes in behaviour have not accompanied declines in physiological or metabolic function, increased foraging experience mask senescence effects (Hassrick et al., 2013; Elliott et al., 2015). Ultimately, as senescence is a within-individual process, longitudinal datasets are needed to disentangle the differences between selective mortality and within-individual changes (van de Pol et al., 2006; Monaghan et al., 2008), as well as the influence of intrinsic quality (Daunt et al., 2006). Nevertheless, this study emphasizes that the ability of individuals to garner resources during the non-breeding period is an important driver of fitness differences, and that the interaction with age deserves further consideration. To follow the behaviour of individuals over extended time periods is logistically challenging (MacNulty et al., 2009), but those studies that manage to do so over consecutive seasons should greatly improve our understanding of the factors influencing senescence in the wild.

Abstract

Senescence has been widely documented in wild vertebrate populations, yet the proximate drivers of age-related declines in breeding success are poorly understood. Foraging performance is likely to be important, as the ability to extract resources from the environment determines the energy that can be allocated to somatic maintenance or reproduction. For long-lived migratory species, the non-breeding period represents a critical time when individuals invest in self-maintenance and restore body condition, yet the relationships between age, foraging behaviour and fitness remain largely unexplored. I investigated age-related variation in the foraging activity, distribution and diet of an extremely long-lived seabird, the wandering albatross *Diomedea exulans* during the non-breeding period, and its links with subsequent fitness metrics. The non-breeding distributions of 82 adults were tracked with geolocator-immersion loggers and age-related declines were found in the average latitude, $\delta^{13}C$ in body feathers, and in the number of landings during daylight hours, a proxy of foraging effort, for both males and females. There was evidence of sexual segregation, with males foraging further south, likely due to their differential utilization of winds. After controlling for the general age-related decline in number of landings, older birds (20+ years) that landed most frequently were more likely to defer breeding or fail during incubation in the subsequent season, whereas younger birds all bred successfully, suggesting that foraging efficiency may be increasingly important in later life. Although longitudinal studies are required to disentangle the influences of selective disappearance and within-individual improvements, as far as I am aware, this is the first demonstration of an age-specific carry-over effect of foraging behaviour in the non-breeding period on subsequent reproductive performance. I conclude that the ability of individuals to forage efficiently outside the breeding period may be an important driver of fitness differences in old age.

6 INDIVIDUAL EXPERIENCE AND IMPROVED PERFORMANCE IN EARLY LIFE SHAPE MIGRATION AND FORAGING STRATEGIES

6.1 Introduction

The period from independence to recruitment as a breeder is a critical life-history stage when mortality rates may be much higher and more variable than in adults. Juveniles are often less skilful than adults and mortality has been linked to poor foraging ability (Lack, 1954; Curio, 1983; Daunt et al., 2007b). Individuals may need to practice in order to become efficient foragers (Marchetti and Price, 1989) and compensate for poor technical ability by increasing their time spent foraging (Sutherland et al., 1986; Daunt et al., 2007b; Riotte-Lambert and Weimerskirch, 2013). Young animals may also exploit different habitats to adults due to differences in morphology, energetic demands or competitive abilities, and in many species, there are marked ontogenetic changes in habitats or trophic ecology (i.e. ontogenetic niche shift; Olson, 1996; Horning and Trillmich, 1997).

In marine species with cryptic life stages, juveniles and immatures are difficult to track and little is known about how individuals develop foraging skills and specializations, including on particular habitats or prey resources (Hazen et al., 2012). Tracking studies have found

increasing evidence of high fidelity of adults to foraging and migratory sites among years (Block et al., 2005; Phillips et al., 2005; Broderick et al., 2007; Arthur et al., 2015), which has lead to suggestions that these are refined on an individual basis through experiential learning in early life (Guilford et al., 2011; Scott et al., 2014). Stable isotope analyses of metabolically inert tissues that grow continuously and are not shed, such as vertebrae, whiskers or teeth, have enabled the documentation of ontogenetic shifts in isotopic niche (Cherel et al., 2009; Authier et al., 2012; Carlisle et al., 2015). However, these methods are limited in that the information provided is generally temporally and spatially coarse, and these methods are not applicable to all taxa (e.g. birds). Evidence from a range of taxa suggests that animals accumulate knowledge about the quality of particular sites, such as physical or biotic features (Brown et al., 2008; Wolf et al., 2009) and so gain familiarity over time (reviewed in Piper, 2011). In particular, individuals are predicted to establish a higher degree of site familiarity in more complex habitats (Piper, 2011), depending on the capacity to learn spatial or other features and the ability to store this information (i.e. spatial memory; Fagan et al., 2013). Given the difficulties of tracking young individuals for long-periods of time (Hazen et al., 2012), few studies are able to observe the ontogeny of movements and foraging decisions of young individuals.

Pelagic seabirds are intriguing study species for examining foraging site selection as juveniles have extremely low movement costs, they have few barriers to dispersal and leave natal sites independently from parents. Recent studies have provided insight into the first c. 6 months at sea, and juveniles tend to use different, usually less productive, regions to adults after leaving the colony (Gutowsky et al., 2014b; Weimerskirch et al., 2006). However, many years may elapse until individuals are seen again (the “lost years”; Hazen et al., 2012), to be followed by a prolonged period of immaturity, when their movements are largely unknown (but see Votier et al., 2010b). This lasts longer in pelagic seabirds that most other avian groups, attributed to the requirement to learn how to forage effectively in an environment in which resources are patchily distributed (Ashmole, 1963; MacLean, 1986). Consequently, it can be assumed that during this period birds learn *how* and *where* to forage, both around the colony and at their non-breeding grounds (Weimerskirch et al., 2013).

In order to investigate ontogenetic changes in movements and foraging behaviour, here I analyse a 13-year, longitudinal tracking study across the early lives of wandering albatrosses *Diomedea exulans*, which as far as I am aware is the first of its kind for any migratory marine

species. Wandering albatross are one of the most oceanic of all seabirds and their distribution includes large swathes of the Southern Ocean (Chapter 5; Weimerskirch et al., 2015), with large among-individual variation in movement strategies (Chapter 2; Weimerskirch and Wilson, 2000). Individual albatrosses were tracked with geolocator-immersion loggers during their post-fledging migrations for up to two years and then again as immatures from the age of 5, and where possible, up to 12 years. Here, I first characterise the ontogeny of movements and at-sea behaviour of first-years, and then of birds across their early lives. In order to determine whether long periods of immaturity are required to learn how to forage (Ashmole, 1963), I investigate changes in at-sea activity patterns with age, in particular the role of within-individual improvement and whether the learning process is gradual or abrupt. Juveniles are predicted to show greater variation in migration routes than adults and become more site-faithful with age (Cresswell, 2014). To test this, I investigate within-individual changes in the size of home ranges and consistency in space use (i.e. site-fidelity) with age, anticipating that birds would gradually canalize site choice over the immature period due to familiarity. Finally, I tested the extent to which individuals were consistent in site use relative to the distribution of individuals within the population.

6.2 Methods

6.2.1 Study site and data collection

Fieldwork was conducted between 2001 and 2013 at a long-term wandering albatross study colony on Bird Island, South Georgia (54°00’ S, 38°03’ W). Chicks have been ringed annually since 1972 and regular monitoring of nests has been conducted since 1980. The breeding cycle of wandering albatross lasts almost 1 year with egg-laying and hatching in December and March, respectively, and fledging of the chick in November–December (Tickell, 2000). Nests are visited daily during the laying, hatching and fledging periods and weekly at other times. The identities of immature and non-breeding birds are checked on a weekly basis.

The non-breeding movements of birds from the same cohort were tracked over multiple years, from fledging and where feasible, throughout immaturity and after recruitment into the breeding population. In November 2001, geolocator-immersion loggers (MK3, 9 g; BAS, Cambridge, UK) were deployed on the tarsus of 58 chicks, in order to track their post-

fledging migrations. When birds returned to the colony 3–6 years later (2004–2007), loggers were retrieved; further deployments of geolocators (MK4–5, 7 and 14, 1.4–5 g) were made on these individuals when resighted from ages 5–12 (2006–2013) (Fig. 6.1). In order to determine whether the sample of tracked birds was representative of the wider population, I compared demographic parameters between tracked and untracked birds. Birds that were tracked as fledglings were from an intensely studied sub-colony and so were more likely to be resighted as immatures than control birds, but not as breeding adults (see Appendix 5 for further details). As a result, I used generalized linear models (GLM) to compare parameters associated with breeding: the probability of having recruited into the breeding population by 2015 (aged 14) (binomial error distribution) and the age of recruitment (Gaussian error distribution). Backwards stepwise model selection was conducted using Akaike Information Criterion (AIC) values. Birds were sexed from field observations (size and plumage dimorphism, copulatory position) or using molecular methods (Froy et al., 2013).

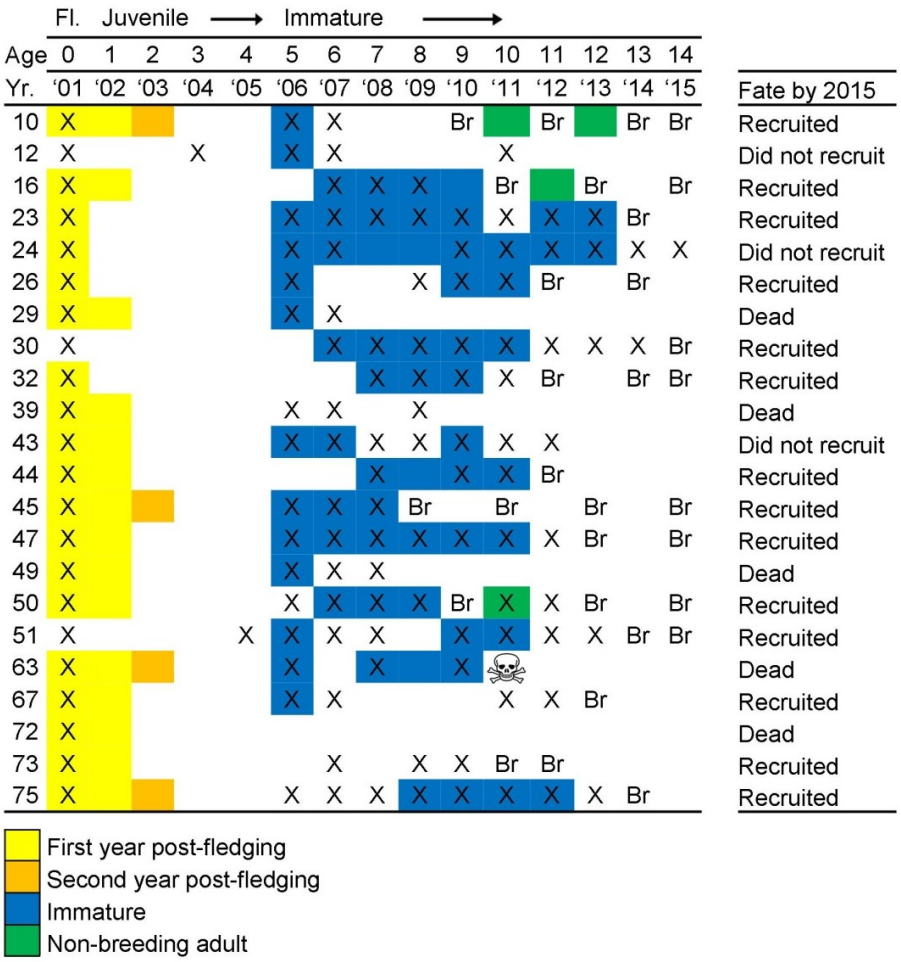


Figure 6.1. Tracking and recapture histories of wandering albatrosses in this study. Geolocator tracking is indicated by a coloured box, resighting at the colony by "X", and a breeding attempt by "Br". A bird was assumed dead by the end of the study if it was not resighted at the colony in the last five years (2011-2015). Two birds were confirmed dead: one (#63) was killed by a Japanese longline vessel in the Atlantic Ocean in 2011 (indicated by skull and crossbones), and the remains of another (#72) was found on a beach in New Zealand. Fl. = Fledging.

6.2.2 Ontogeny of movements and spatial consistency

Light data were processed using MultiTrace Geolocation (Jensen Software Systems) or BASTrak software (British Antarctic Survey, Cambridge, UK), providing two positions per day with a mean error 186 ± 114 km (Phillips et al., 2004b). Locations with interruptions around sunrise and sunset and periods around the equinox (3 to 4 weeks), when latitude cannot be estimated reliably, were excluded. For each individual and year, defined as December–November to match the temporal extent of the breeding season, I created 50% and 95% utilization distributions (UDs) within the R package *adehabitat* (Calenge, 2006) to represent core and general use areas, respectively (Lascelles et al., 2016). I specified bivariate normal kernels using a grid size of 50 km and a smoothing parameter of 200 km to account for geolocator error (Phillips et al., 2004b, 2005). It was hypothesized that unlike adult birds, which migrate to discrete foraging areas (Chapter 5; Weimerskirch et al., 2015), naïve juveniles would perform large-scale exploratory movements (Riotte-Lambert and Weimerskirch, 2013) and so the size of their core areas would be larger than older birds. However, if birds did not change their migration strategy substantially with age, there should be no change in the size of general use areas. To test this hypothesis, linear mixed models (LMM) were implemented within the *lme4* package in R (Bates et al., 2015) with individual identity included as a random effect, in order to partition within- and between-individual differences (van de Pol et al., 2006). Models were run for birds tracked for 3+ years with age, separately for core and general use areas. Age was fitted as a linear fixed effect and if significant, models containing a range of break points were compared with AIC values to determine if there was a threshold with age, as it might be predicted that the size of core areas would asymptote at a particular age threshold (Berman et al., 2009; Froy et al., 2013).

Secondly, I investigated the relationship between age and the overlap of spatial distributions, testing the hypothesis of increased spatial overlap with age, and by inference, of increased fidelity to particular sites. I calculated within-individual consistency in space use between UDs in multiple years using Bhattacharyya's affinity (BA, Fieberg and Kochanny, 2005), which ranges between 0 (no similarity between UDs) and 1 (identical UDs i.e. completely consistent). Following Wakefield et al. (2015), the overlap between two years (Yr_1 and Yr_2) for the *i*th individual is:

$$BA_{x,y,i} = \sum_{x,y} \sqrt{UD_{i,Yr_1}(x,y) UD_{i,Yr_2}(x,y)}$$

where *x* and *y* are longitude and latitude in Cartesian space. Spatial overlap scores were calculated for core (50% UD) and general use (95%) areas using the kerneloverlaphr function in the *adehabitat* package (Calenge, 2006). While this metric compares annual distributions, it does not indicate consistent use by individuals of particular regions at given times of the year. As such, I also used a metric of spatio-temporal consistency, nearest neighbour distances (NND), modified from Guilford et al. (2011). For each day of a focal track, I iteratively calculated the distance to its neighbour on a comparison track, smoothing locations over a 10-day window to reduce the influence of anomalous locations associated with geolocation error (Phillips et al., 2004b). Distances between tracks were calculated within the R package *geoGraph* (Jombart et al., 2013), which uses graph theory to calculate the least cost path between two points. Distances can be calculated without the need for projections and multiple cost layers can be integrated; here, paths were not allowed to pass over land or sea-ice (See Appendix 5 for further details). The advantage of using NND is that it can also infer route fidelity (Guilford et al., 2011). For example, a bird that travels to several regions, albeit at completely different times of the year, would be classified as consistent from the UDs, yet the average distance between the pairwise locations might always be large, indicative of low spatio-temporal consistency.

Accordingly, I tested the hypothesis that birds would become increasingly consistent in both space and time with increasing age, using a) only consecutive years, and b) all pairwise combinations of years. The first set of analyses explored changes in the overlap of pairs of years that were only one year apart, i.e. 2002 and 2003, 2006 and 2007, 2007 and 2008 etc. The second set of analyses used all available combinations of years, i.e. 2002 and 2003, 2002 and 2006, 2002 and 2007 etc., to test for an obvious shift in the space use of individuals

between life stages, i.e. from juvenile to immature stages. For both sets of analyses, the fixed effect of age refers to the age of the individual in the earlier of the two years; while for analyses using all year combinations, the difference in age between the two years was also included as a fixed effect. Analyses were carried out separately for the core and general use areas and for NND. Data were log- or square-root transformed to improve normality assumptions, where necessary. As above, models containing the linear effect of age were compared with those containing a range of break points to determine if they improved model fit.

6.2.3 Individual consistency in space use

Additionally, I tested to what extent individuals were consistent in their distributions as immatures. Spatial consistency was quantified at the individual-level relative to the population using a randomization procedure, with the null hypothesis that within-individual consistency was greater than population-level consistency (Nakagawa and Schielzeth, 2010; Wakefield et al., 2015). Analyses were conducted using data for birds tracked for 3+ years during immaturity (See Appendix 5 for further details). The randomization procedure was tailored to control for unequal sampling (Fig. 6.1), whereby null distributions were generated for each individual based on the combinations of years for which they were tracked. For each pairwise combination of years, two random tracks were selected from a pool of all individuals tracked in those two years and their spatial overlap calculated. The mean of all combinations of years was then calculated. This procedure was carried out 1,000 times to generate a randomized distribution for each individual, which was compared to the mean of all pairwise combinations of spatial overlap for that individual. Analyses were conducted for BA overlap scores at the core and general use level, and for NND; *P*-values were determined as the proportion of randomized overlaps that were greater than the observed for BA overlap metrics and smaller than the observed for NND (Chapters 3-5). All analyses were conducted in R v. 3.3.1 (R Core Team, 2014). Unless otherwise reported, data are presented as means ± standard deviations (SD).

6.2.4 Ontogeny of at-sea behaviour

Loggers tested for saltwater immersion every 3 s storing the sum of positive tests at the end of each 10 min period providing a value ranging from 0 (continuously dry) to 200 (continuously wet). Each period was categorised as daylight or darkness based on the timing

of civil twilight from the light data. A wet bout was defined as a 10 min period, during which at least one wet event was recorded and a flight bout as a continuous 10 min period spent entirely dry. I selected the following at-sea activity metrics: the proportion of time spent flying (dry) and number of landings (wet bouts) per hour, as flight activity and landing rates are important drivers of energy budgets in albatrosses (Weimerskirch et al., 2000a; Shaffer et al., 2001a) (see Chapter 5), and length of wet bouts as long periods spent on the water are likely associated with resting or digestion of prey (Weimerskirch and Guionnet, 2002). Each metric was calculated for both daylight and darkness periods combined, as well as separately (Weimerskirch et al., 2005).

I investigated ontogenetic changes in behaviour at two temporal scales; over the first year since fledging (2001- 2002) and across all years of tracking (2001-2013). Age was expressed as a fixed effect up to the third order polynomial to investigate non-linear patterns. For first-years, age was modelled as the number of months since the fledge date. Median monthly values of each metric were extracted, and only individuals with at least 5 months of data were considered. Models of all years included only individuals with at least 3 years of data. Initial data visualization indicated that activity patterns of immatures were dominated by dry periods spent at the colony, particularly in January-May (Pickering, 1989; Weimerskirch et al., 2013). As a result, I only considered data for immature birds during their migration phase, excluding data from periods spent on or around the colony, defined using immersion data (see Appendix 5 for details). Logger battery failure limited data coverage across some years and, in order to account for incomplete sampling, data were averaged for each month, and month was included as a categorical factor to control for changes in activity according to photoperiod. In all models, sex was included as a predictor variable. The proportion of time spent flying was arcsine transformed and for other response variables, data were log- or square-root transformed to improve data spread, where necessary. For all model comparisons, I used AIC values to rank all possible model combinations according to their degree of parsimony. Where multiple models were within 2 AIC units of the best supported model, the most parsimonious model (with the fewest parameters) was chosen (Arnold, 2010; Burnham and Anderson, 2004). Predictions were made at the population-level by predicting across individuals using the R package *merTools* (Knowles and Frederick, 2016) and averaging predictions to control for variation in individual responses. Models were also run using the raw metrics not controlled for photoperiod (i.e. number of hours spent dry per day and number of landings per day) for comparison (see Table A5.1, Fig A5.5). I also investigated

changes in the migratory schedules of immature birds with age, focussing on the dates of departure from, and arrival at the colony, based on the timing of directed movements (Guilford et al. 2009).

6.3 Results

6.3.1 Longitudinal tracking

Over the course of the study (2001–2013), 88 years of tracking data were collected from 22 individuals (Fig. 6.1, See Appendix 5 for deployment and retrieval details). For 15 individuals there were data on the first year at sea and 19 individuals were tracked as immatures for up to 8 years. On average, birds were tracked for 4 ± 2 years (n = 22), including for 3 ± 2 years (n = 19) as immatures. There were no differences in the probability of recruitment into the breeding population of tagged and non-tagged birds (tagged birds: 26%, n = 15; non-tagged birds: 26%, n = 147; ΔAIC = 2.01, χ_1^2 = <0.01, P = 0.99) by the end of the 2015 breeding season, and nor was there a significant difference in the mean age of recruitment (tagged = 11.0 ± 1.8 years, non-tagged = 10.4 ± 1.7 years; ΔAIC = 0.37, χ_1^2 = 4.88, P =0.19). These results suggest that the tracking sample was representative of the wider population.

6.3.2 Ontogeny of movements and spatial consistency

The tracked birds fledged on 6 December 2001 ± 10 days (n = 58, range = 17 November – 30 December) and generally remained around the colony for the first few days before moving north into subantarctic and subtropical waters (Fig. 6.2a, A5.4). By the end of the 3rd week post-fledging, there was substantial among-individual variation in both the trajectory and distance travelled from the colony, with some birds migrating eastwards towards the southeast Atlantic, others northwest towards the Patagonian Shelf, and the majority to the north of the colony (Fig. 6.2a, A5.4). After only two months, many juveniles had dispersed around the Southern Ocean, one as far as New Zealand (Fig. 6.2b). At this point there appeared to be two dominant strategies, either dispersal into and east of the Indian Ocean, or residency in the southwest Atlantic Ocean (Fig 6.2b, A5.4). By July, many of those previously in the southwest Atlantic had moved east into the southeast Atlantic or the Indian Ocean, those previously in the Indian Ocean had moved east into the Pacific Ocean or west

into the Atlantic Ocean, and one individual had completed a full circumpolar migration back to South Georgia (Fig. 6.2c). Indeed, by the end of its first year, that individual had conducted two circumpolar migrations. By the end of their first year, 6 (40%) had passed 180° in longitude, indicating likely circumpolar migrations (logger batteries typically failed thereafter). During the first year, juveniles predominantly used pelagic waters around and to the north the Subtropical Front (Fig. 6.3a); in contrast, the four birds tracked in their second year utilised areas closer to continental shelves or shelf breaks, off the Humboldt Current and Patagonian Shelf (Fig. 6.3b). After 2-5 years at sea, birds returned to the colony for the first time; they subsequently spent the first third to half of the year in the southwest Atlantic (Fig. A5.5), with regular visits to the colony, and the latter half of the year in the southwest Indian Oceans and around New Zealand (Fig. A5.5), and around the southeast Pacific and southwest Atlantic Oceans (Fig. 6.3c), which are all major non-breeding destinations of adult birds (Chapter 5).

During the immature phase, birds departed on their migrations in March–April, until they reached c. 9 years old, after which departure dates generally advanced to January–February; explained best by the cubic relationship of age (Fig. 6.4a, Table A5.3). Birds also gradually advanced their arrival date back at the colony by around a week for each increasing year, until they arrived in line with non-breeding adults (Chapter 2) at 9 -10 years old (Fig. 6.4b). This relationship was explained best by the linear effect with age (Fig. 6.4b, Table A5.3). There was no effect of sex on arrival or departure dates (Table A5.3).

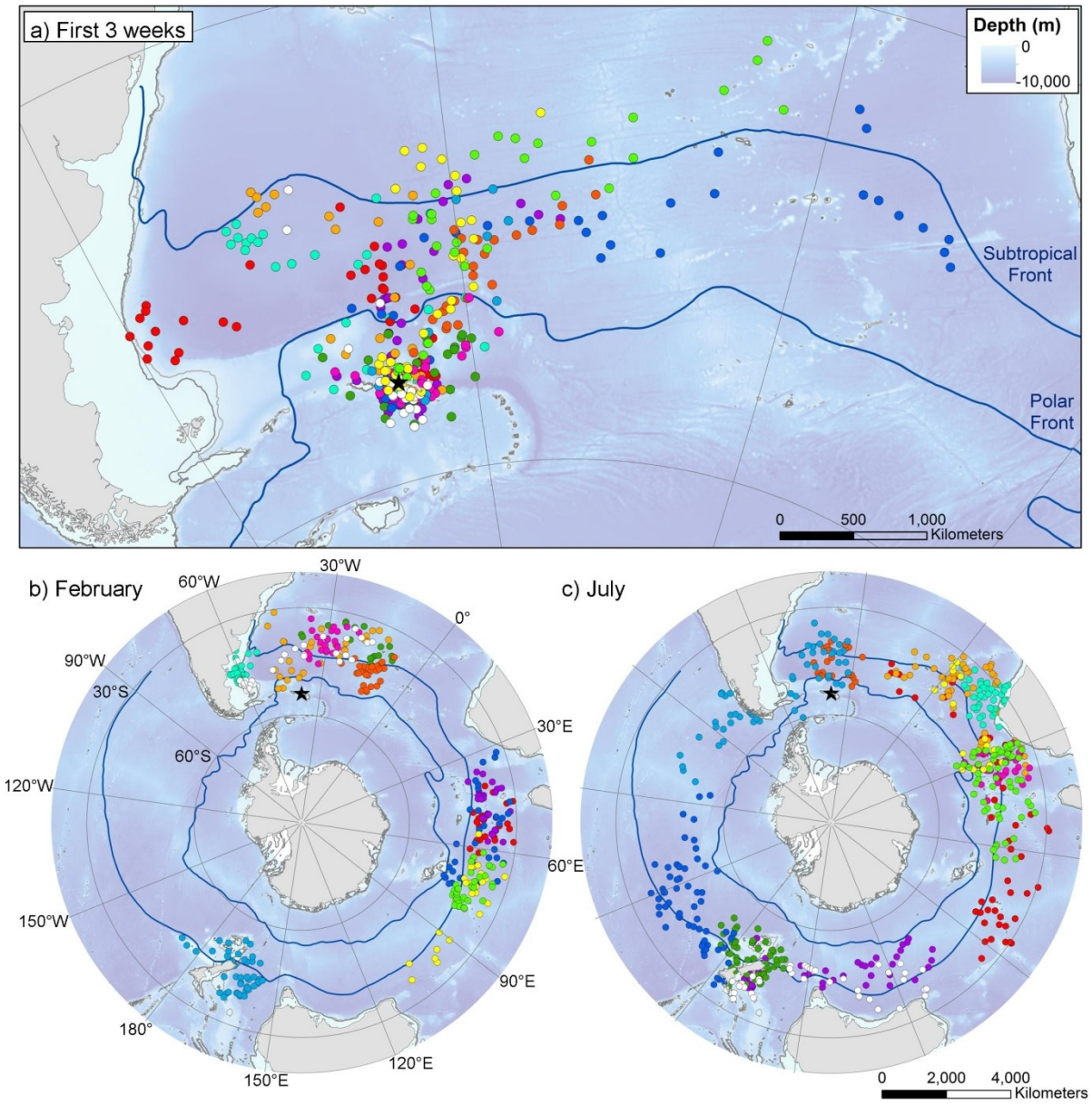


Figure 6.2. The post-fledging dispersal strategies of 12 representative wandering albatrosses tracked with geolocators from Bird Island, South Georgia (black star). Locations are coloured differently for each individual and are shown for: a) the first 3 weeks since fledging, b) February (c. 2 months post-fledging) and c) July (c. 7 months post-fledging). The 500 m and 1,000 m isobaths are shown by dark and light grey lines, respectively.

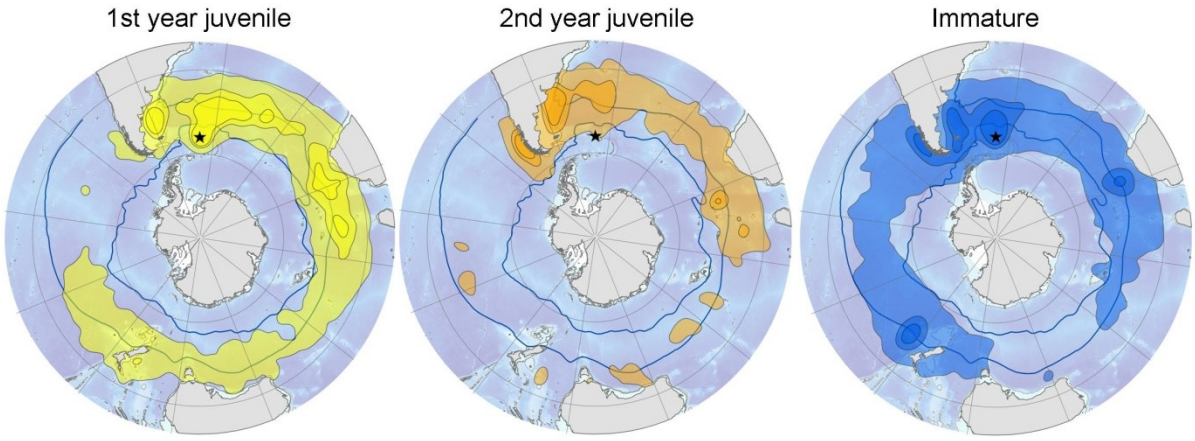


Figure 6.3. The core (25% and 50%) and general use (95%) utilization distributions (UDs) of first (yellow, n = 15) and second-year juvenile (orange, n = 4) and immature (blue, n = 66) wandering albatrosses tracked with geolocators from Bird Island, South Georgia (black star). The average positions of the Subtropical and Polar Fronts are shown with dark-blue lines.

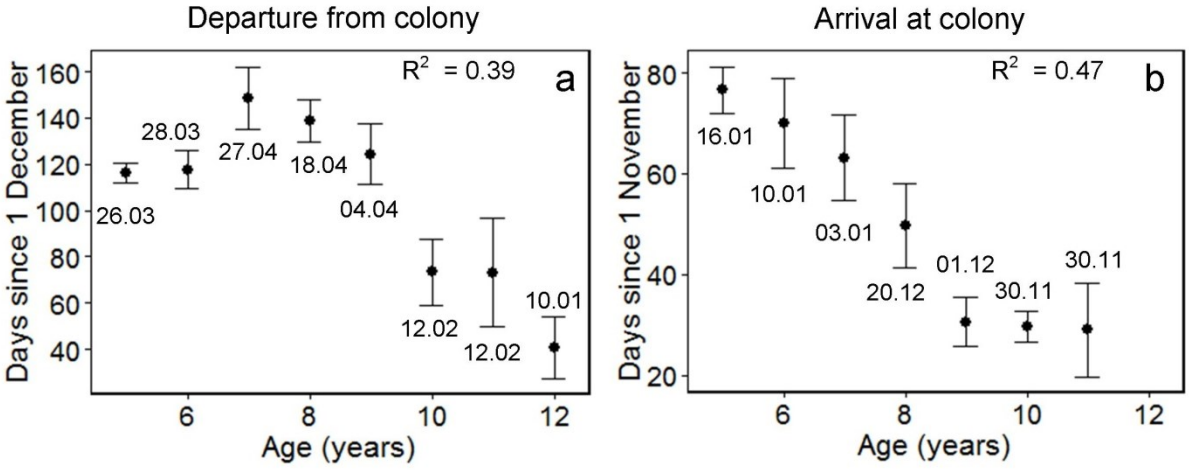


Figure 6.4. The relationship between age and the migratory schedules of immature albatrosses: a) departure from, and b) arrival at the colony. For each age, means are shown ± standard error and the variance explained by age is displayed (marginal R^2).

I investigated the relationship between age and the size of core and general use areas, and as predicted, there was a decrease in the size of core areas, but no change in the size of general use areas with age (Fig. 6.5, Table 6.1). The relationship between age and core area was best explained by a breakpoint after the first year at sea, indicating that foraging areas reduced in size (Table A5.4). Secondly, I investigated the relationship between age and the overlap of spatial distributions in consecutive years. Contrary to the prediction, there was no age effect

on the spatial overlap of core or general use areas, or nearest neighbour distances (NNDs) (Fig. 6.6, Table 6.1). These analyses were expanded to investigate the spatial overlap between combinations of all years. As predicted, there was a significant increase in the spatial overlap between core and general use areas, and a decrease in NNDs with increasing age (Fig. 6.7, Table A5.5). There was also decrease in spatial overlap of core and general use areas with an increasing age difference; however, the difference with age was not significant for NNDs (Table 6.1, A5.5). The effect of age was best explained by a linear relationship (Table A5.6). These results suggest that the increasing consistency in site use over the course of early life is gradual, such that differences are not detected from one year to the next but only after longer intervals. For both sets of analyses, a large proportion of variance was explained by the random effect of individual, suggesting large variability among individuals in their response with age (Table 6.1).

Table 6.1. Results of linear mixed-effects models investigating ontogenetic changes in the size of home ranges and spatial consistency of wandering albatrosses tracked with geolocators throughout their early lives.

	Response	Predictors		df	AICc	ΔAICc	R^2	R^2
		$Yr_{Diff.}$	Age				marginal	conditional
Area of home ranges								
	50% UD	n\a	X*	4	313.7	0.00	0.16	0.31
	95% UD	n\a	–	3	575.9	0.00	0.00	0.32
Spatial consistency								
Yr_{Paired}	50% UD	n\a	–	3	-67.5	0.00	0.00	0.31
	95% UD	n\a	–	3	-32.4	0.00	0.00	0.54
	NND	n\a	–	3	320.2	0.87¥	0.00	0.42
Yr_{All}	50% UD	X	X	5	98.11	0.00	0.19	0.43
	95% UD	X	X	5	-168.7	0.00	0.19	0.53
	NND	–	X	4	1436.5	0.00	0.16	0.54

*Analyses of spatial consistency were carried out using metrics of spatial overlap of distributions using consecutive years of tracking (Yr_{Paired}), and using all combinations of years (Yr_{All}). The latter analyses included a variable ($Yr_{Diff.}$) controlling for the difference in years between the two distributions. NND = nearest neighbour distances. For spatial consistency analyses, age refers to the younger of the two years used to calculate spatial overlap. * = age modelled with breakpoint that better explained relationship of age; ¥ = another model had a lower AICc, but not to the extent of incurring the penalty of extra parameters.*

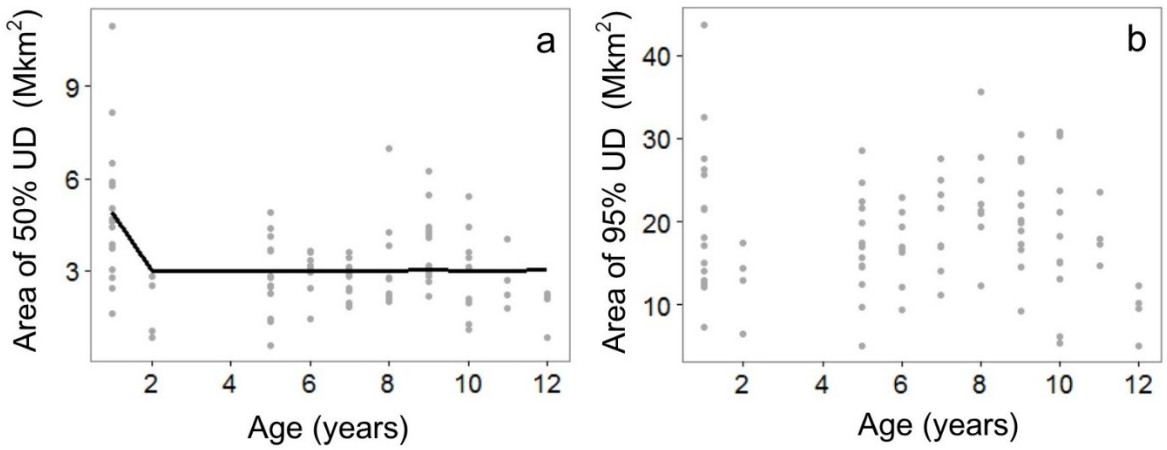


Figure 6.5. Ontogenetic changes in the size of core (50%) and b) general use (95%) utilization distributions of wandering albatrosses tracked with geolocators. Significant effects of age are shown by a predicted black line of best fit, averaged among individuals to control for variation. Mkm^2 = millions of square kilometres.

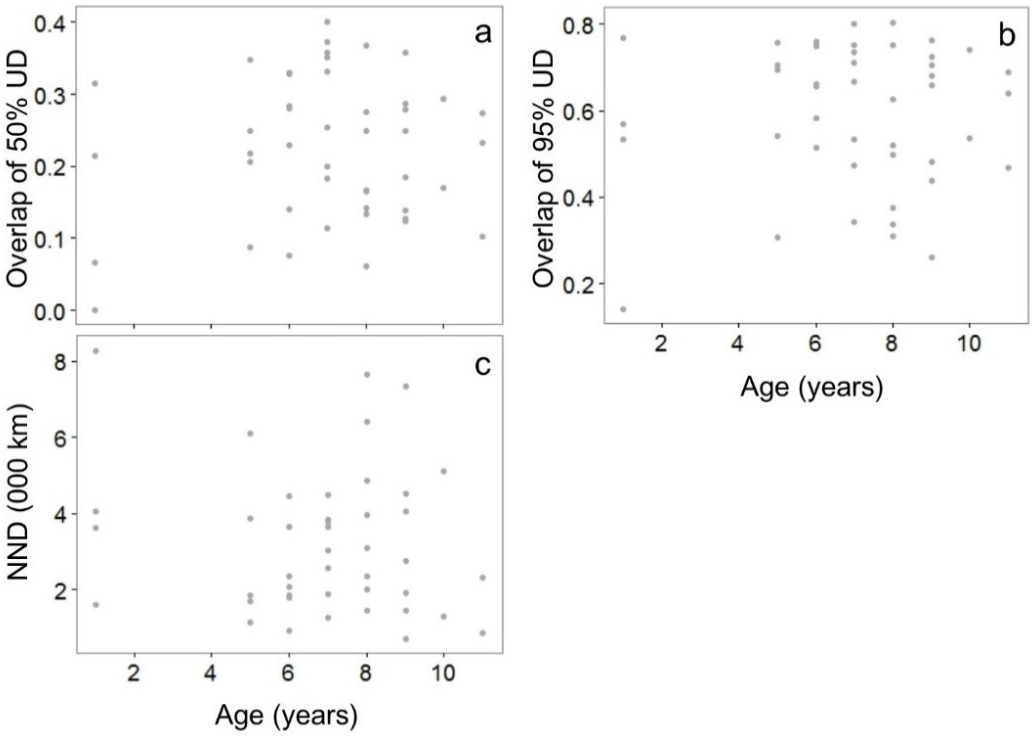


Figure 6.6. Figure 6.6. Ontogenetic changes in the the spatial consistency of distributions in consecutive years of wandering albatrosses tracked with geolocators; the spatial overlap (Bhattacharyya's Affinity [BA]) of a) core and b) general use areas, and c) the average distance between two locations in consecutive years at a given time of year (nearest neighbour distances [NNDs]). Age represents the minimum of the two

years used to calculate overlap scores. Significant effects of age are shown by a predicted black line of best fit, averaged among individuals to control for variation.

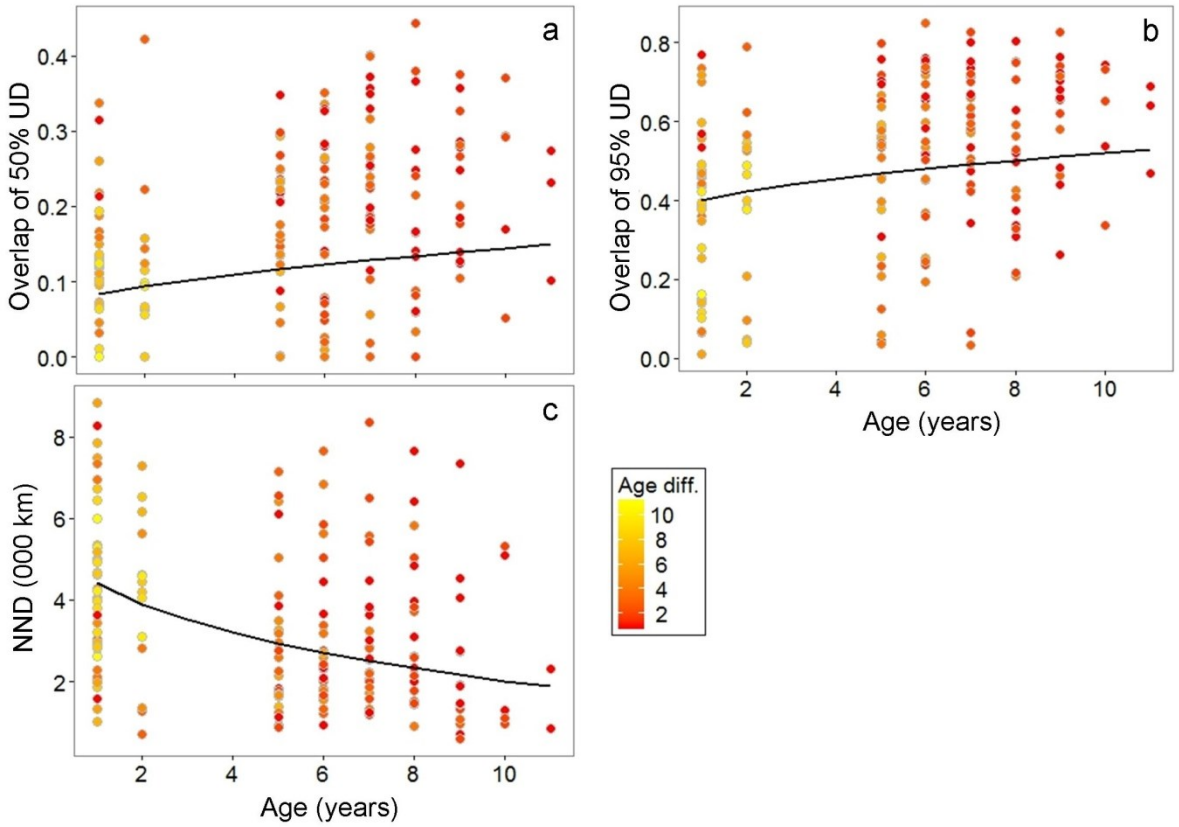


Figure 6.7. Ontogenetic changes in the spatial consistency of wandering albatrosses tracked with geolocators, using all pairwise combinations of years. The spatial overlap (Bhattacharyya's Affinity [BA]) of a) core (50%) and b) general use (95%) utilization distributions (UDs), and c) the average distance between two locations at a given time of year (nearest neighbour distances [NNDs]). The age of the younger of the two years is shown along the x-axis and the difference in age between years represented by a colour gradient. Significant effects of age are shown by a predicted black line of best fit, averaged among individuals to control for variation.

6.3.3 Individual consistency in space use

I carried out a randomization procedure to determine how consistent individuals were in their movements and distributions. Of the 14 birds tracked for 3+ years as immatures, seven (50%) were consistent in core areas (50% UD) and nine (64%) were consistent in general use areas

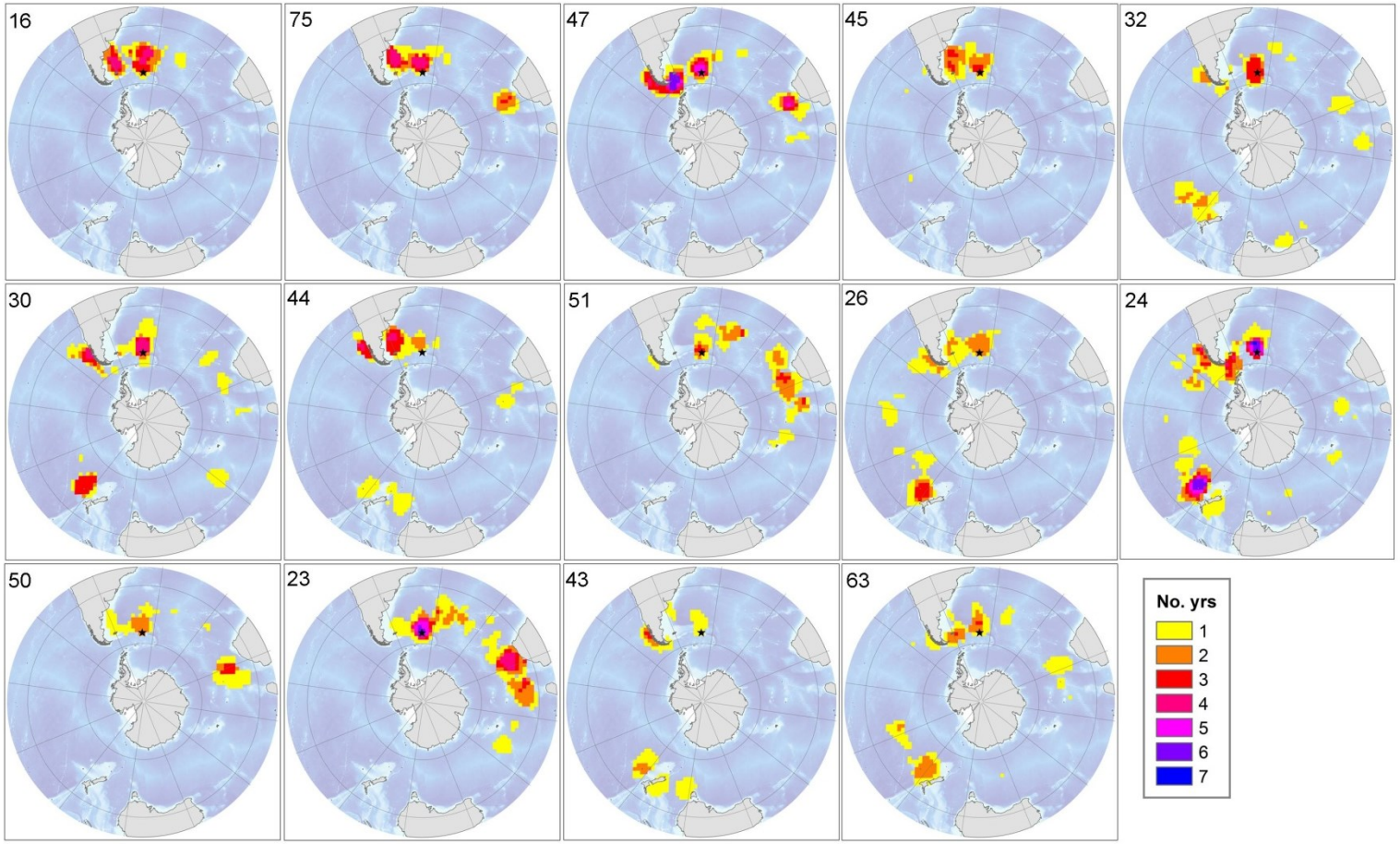
(95% UD) and in space and time (NND) (Fig. 6.8, Fig. A5.6). Examples of varying levels of individual consistency in migration strategies are shown in Fig. 6.9. Some individuals consistently used particular ocean regions at specific times of the year, such as the southwest Indian Ocean or New Zealand in the austral winter or the Humboldt Current at the start of summer, and areas repeatedly visited were often those first visited by birds in their first year at sea (Fig. 6.9, A5.6). While birds were generally more consistent in their movements than expected by chance (Fig. 6.8), these movements were not necessarily fixed, such that some individuals varied their use of foraging areas both within and between years (Fig. 6.9).

6.3.4 Ontogeny of at-sea behaviour

All of the best supported models explaining the at-sea activity patterns of albatrosses in their first year post-fledging included the effect of age (Table 6.9). In the first month post-fledging, birds were the least active, but over the first 4-5 months, birds increased their flight activity, particularly during daylight hours (Fig. 6.10a). The proportion of time in flight during daylight peaked at 3-6 months post-fledging. In contrast, birds took longer to increase their flight activity during darkness, with flight activity peaking 6-7 months post-fledging, but this is likely to be influenced by seasonal changes in day length. During their first year, birds maintained a similar level of daily (including daylight and darkness) hours in flight from *c.* 4 months onwards (Fig. A5.3). As birds became more active, the length of wet bout lengths during daylight and darkness decreased accordingly (Table 6.2, Table A5.1). During the first month post-fledging the landing rate (number of landings per hour) during daylight and darkness was substantially lower and higher, respectively, than the rest of the year (Fig. 6.10ac). By the 2nd month post-fledging, the daily landing rate (including daylight and darkness) appeared to plateau and subsequently followed a linear decrease over the rest of the first year at-sea.

There was a significant effect of age in 7 out of 8 metrics tested during all years of tracking (Table 6.2). Indeed, the linear decrease in landing rate in their first year continued across the first 11 years of life, for both daylight and darkness periods separately and combined (Fig. 6.10a, d). Similarly, birds decreased the amount of time spent in flight during daylight and during daylight and darkness combined; however, there was no age effect when darkness periods were considered separately (Fig. 6.10a, b). Accordingly, the length of wet bouts increased (Table 6.2, Table A5.1), during both daylight and darkness hours.

a)



b)

	Id														
	16	75	47	45	32	30	44	51	26	24	50	23	43	63	% consistent
No. years tracked as immature	4	4	6	3	3	5	4	3	3	8	3	7	3	4	-
Overlap among core areas	0.30	0.28	0.27	0.26	0.23	0.20	0.19	0.19	0.18	0.18	0.17	0.15	0.09	0.05	**50%**
Overlap among general use areas	0.77	0.74	0.68	0.75	0.51	0.46	0.59	0.63	0.54	0.49	0.59	0.55	0.34	0.20	**64%**
Nearest neighbour distances (km)	1627	1064	2209	1449	4996	5199	2470	1754	2523	3363	1283	2240	4138	5421	**64%**

P value	
	< 0.001
	< 0.01
	< 0.05
	n.s.

Figure 6.8. a) The core distributions (50% UDs) of 14 individual wandering albatrosses tracked for 3–8 years as immatures. b) The overlap index scores (Bhattacharyya's affinity, BA) for core and general use (95% UD) areas, and nearest neighbour distances (NND) are shown for each individual. Where an individual is consistent, the cell is filled in gray-scale according to the level of significance.

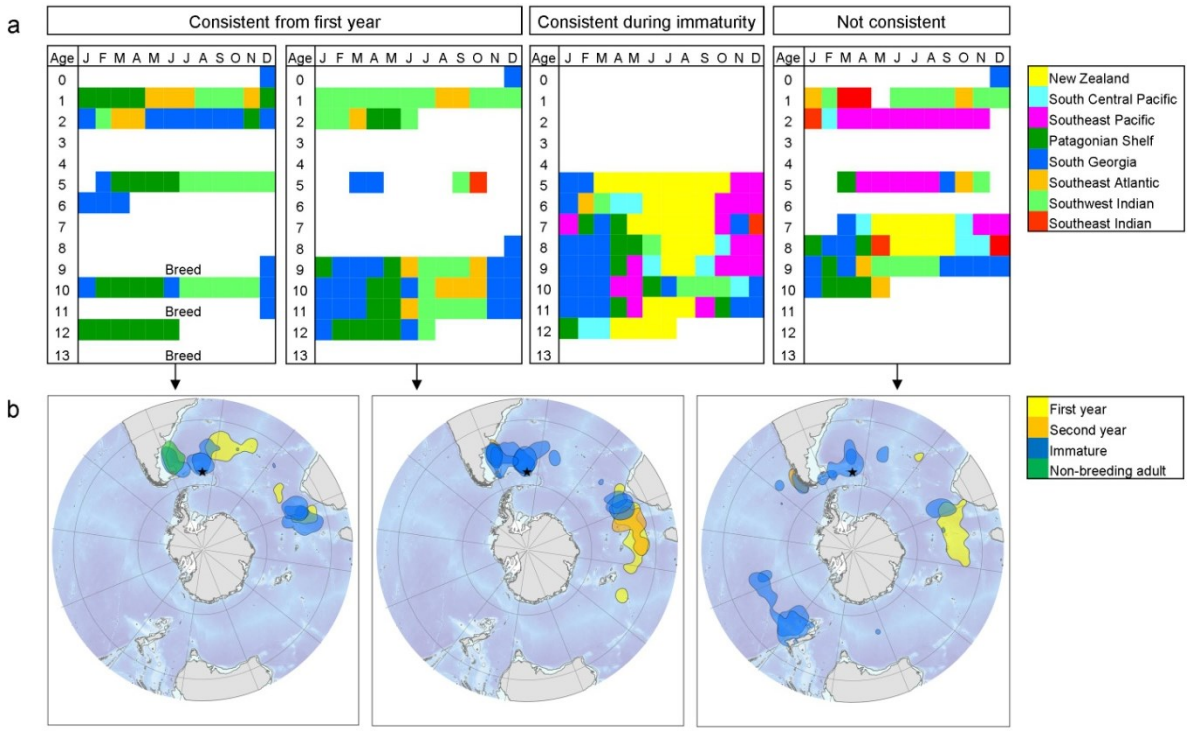


Figure 6.9. a) Examples of individual consistency in the use of ocean sectors by wandering albatrosses tracked with geolocators at particular times of the year, and b) their annual core (50%) utilization distributions (UDs). Plots in top pane show the most intensely used sector (based on longitudinal thresholds; Fig. A5.7) for each month. First year data for the third individual shown in the top pane lasted less than two weeks and so is not shown.

While there were no sex differences in activity metrics across the first year, there was a significant effect of sex in models of activity metrics across all years, but only during darkness (Table 6.2). Females spent more time in flight, had a higher landing rate and shorter wet bouts than males during darkness (Table A5.1). The large proportion of variance explained by the random effect of individual identity suggests that there was large among-individual variability in activity patterns, particularly during the first-year at sea (Table 6.2).

For the most part, results of models using raw values matched those using proportions, suggesting that the results are robust to use of different metrics (Table A5.2).

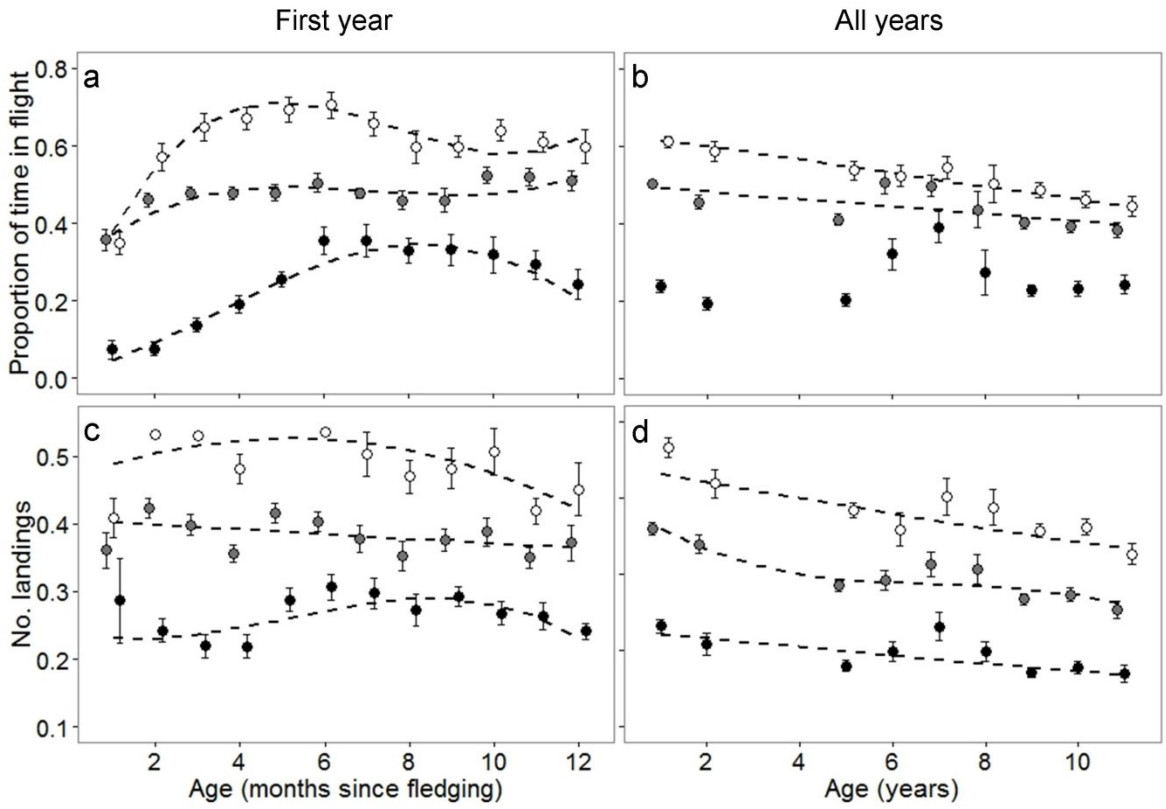


Figure 6.10. Ontogenetic changes in (a-b) flight (proportion of time spent flying) and (c-d) foraging activity (number of landings per hour) of wandering albatrosses tracked with geolocators. The left and right panes show activity in first year and the first eleven years, respectively. Activity during daylight (open circles), darkness (black circles) and for both periods combined (grey circles) are shown ± standard error, with the relationship of age predicted from models, shown where significant as dashed lines, and averaged across individuals to correct for individual variation.

Table 6.2. Results of linear mixed-effects models investigating ontogenetic changes in the activity patterns of wandering albatrosses tracked with geolocators during their first year post-fledging, and in the first eleven years.

Time period	Response variable	N	Predictor variables					df	AICc	ΔAICc	R^2 marginal	R^2 conditional
			Age	Age^2	Age^3	Sex	Month					
First year	Time in flight (%)	12 (125)	X	X	X	–	n\a	6	-289.0	1.96*	0.20	0.36
	Time in flight daylight (%)	12 (125)	X	X	X	–	n\a	6	-182.3	1.40*	0.38	0.56
	Time in flight darkness (%)	12 (125)	X	X	X	–	n\a	6	-180.2	0.00	0.51	0.70
	No. landings hr^{-1}	12 (110)	X	–	–	–	n\a	4	-320.9	0.28*	0.03	0.19
	No. landings hr^{-1} light	12 (110)	X	X	–	–	n\a	5	-227.5	0.00	0.10	0.36
	No. landings hr^{-1}dark	12 (110)	X	X	X	–	n\a	6	-308.0	0.00	0.10	0.35
	Wet bout length light (hrs)	11 (115)	X	X	X	–	n\a	6	210.0	0.00	0.15	0.15
	Wet bout length dark (hrs)	11 (115)	X	X	–	–	n\a	5	139.5	1.81*	0.39	0.55
All years	Time in flight (%)	14 (58)	X	–	–	–	X	15	-607.7	1.02*	0.23	0.25
	Time in flight daylight (%)	14 (58)	X	–	–	–	X	15	-316.7	0.00	0.20	0.23
	Time in flight darkness (%)	14 (58)	–	–	–	X	–	4	-209.5	0.00	0.04	0.08
	No. landings hr^{-1}	14 (57)	X	X	X	–	X	17	-979.9	1.19*	0.27	0.29
	No. landings hr^{-1} light	14 (57)	X	–	–	–	–	4	-18.3	0.98*	0.13	0.18
	No. landings hr^{-1}dark	14 (57)	X	–	–	X	–	5	-874.0	0.51*	0.12	0.12
	Wet bout length light (hrs)	14 (57)	X	–	–	–	X	15	724.9	0.97*	0.23	0.26
	Wet bout length dark (hrs)	14 (57)	X	–	–	X	–	5	1104.7	1.69*	0.06	0.06

The linear, quadratic and cubic relationships of age were modelled for each month and year since fledging for analyses of the first year and all years, respectively. Analyses of all years also included monthly values and month was included as a fixed effect. Only the most parsimonious models are shown. N =

*number of individuals with the number of months or years shown in parentheses for analyses of the first year or all years, respectively; X = predictors that were retained in the most parsimonious models; – = predictors not retained; n\a = not tested; AICc = Akaike information criterion corrected for small sample sizes; * = another model had a lower AICc, but not to the extent of incurring the penalty of extra parameters.* $R^2_{marginal}$ *= proportion of variance explained by the fixed effects, and* $R^2_{conditional}$ *= by the fixed and random effects.*

6.4 Discussion

6.4.1 Ontogeny of foraging site selection

The movement patterns of the tracked albatrosses can be split into two distinct phases, which I discuss in turn: dispersal from the natal colony to distant foraging grounds, and the process of gradual refinement of foraging areas with age. After leaving their natal colony, birds remained around South Georgia, potentially waiting for suitable winds, before travelling north-northeast until they crossed the Polar Front into subantarctic and subtropical waters, following the same bearing relative to the colony as fledglings at Crozet and Kerguelen (de Grissac et al., 2016). As juveniles depart the colony at various times between mid-November and mid-December without the assistance of their parents, which generally depart earlier and in multiple directions (Weimerskirch and Wilson, 2000), the initial dispersal process and direction appears to be innate (Åkesson and Weimerskirch, 2005; Weimerskirch et al., 2006). The northward movement of the albatrosses takes them into subtropical waters, where they show little apparent spatial overlap with adult non-breeders (Chapter 5). The use of less productive waters by juveniles has also been found in other seabird species (Péron and Grémillet, 2013; Gutowsky et al., 2014b) and, in wandering albatrosses, is presumably a mechanism to reduce competition with adults (Weimerskirch et al., 2006). Juveniles also have longer wings than adults (Weimerskirch et al., 2000b), a possible adaptation to flight in subtropical waters, which are much less windy than regions used by adults further south (Weimerskirch et al., 2000b; Shaffer et al., 2001b).

The second phase of dispersal, when the tracked birds differed greatly in their flight directions and distances travelled (also see Weimerskirch et al., 2006), is likely to be driven by individual experience and response to local conditions, although some birds may be more inclined than others to move with the prevailing wind, which is from the west. After six months at sea, the tracked juveniles had dispersed into all Southern Ocean basins, and one individual had conducted a circumpolar trip back to South Georgia. This contrasts with the movements of juveniles from Crozet, which were restricted to the Indian Ocean and Tasman Sea (Weimerskirch et al., 2006). The population-level differences in juvenile distributions appear to match those of adults (Chapter 5, Weimerskirch et al., 2015), which suggests that first-year movements may be important in determining future non-breeding distributions. A

comparison of juvenile and adult distributions from all populations would provide some insight into the relative importance of genetic and environmental factors in driving this striking variation in dispersal patterns.

I found no differences in the recruitment rates of study and control birds, suggesting that the tracking sample was demographically representative of the wider population. However, one major limitation of this study and other longitudinal studies using geolocators is that they require the loggers to be retrieved, which may bias samples towards representing only individuals with successful strategies (but see Daunt et al., 2007b; Orgeret et al. 2016). Longitudinal deployment of satellite transmitters is likely to be prohibitively expensive, but is recommended for determining the causes of mortality events in highly mobile species (Klaassen et al., 2014; Sergio et al., 2014).

Ontogenetic changes in habitat use (i.e. ontogenetic niche shift), and broad latitudinal shifts with age have been found in many pelagic species, including wandering albatrosses (Weimerskirch et al., 2013; Jaeger et al., 2014; Carlisle et al., 2015). Comparisons are usually made between animals of different life stages or through stable isotope analysis of tissues that are metabolically inert or have slow turnover rates (vertebrae, teeth, baleen; e.g. Cherel et al., 2009). While the latter approach enables the documentation of individual changes in diet or habitat selection over long time periods, it provides little of the detail on site selection that can be gleaned from longitudinal deployment of devices. Here, I document that individuals gradually refine their choice of foraging areas with increasing age. Foraging areas were most extensive in the first year and, as predicted, decreased in size with age (Cresswell, 2014). Although only four birds were tracked during their second year at sea, core areas were more concentrated around upwellings and shelf-breaks and were notably smaller than during their first year. This indicates that by this stage, some birds had already located suitable foraging grounds, where they remained for many months. Logger battery failure restricted the data available for the rest of this period at sea, which may be an important phase of exploration. Regardless, individuals became increasingly faithful to their foraging areas during these early stages, and during the subsequent years when data collection recommenced, many immature birds (50% of individuals or higher, depending on the consistency metric) were consistent relative to the population, suggesting that they had by then become faithful to particular sites.

Site fidelity, the repeated use of a previously occupied area (Switzer, 1993), has been found in a range of taxa (Greenwood, 1980; Rydell, 1989), including many marine predator species

(Broderick et al., 2007; Call et al., 2008; Patrick et al., 2013), and is predicted to be directly linked to resource predictability (Switzer, 1993). Accordingly, a study of New Zealand fur seals *Arctocephalus forsteri* found site fidelity was higher in individuals that foraged on more predictable continental shelf rather than oceanic habitats (Baylis et al., 2012). However, while a recent study found evidence of both individual habitat and spatial consistency in northern gannets *Morus bassanus*, the two did not appear to be correlated, suggesting that resource predictability may not be the main driver of site fidelity (Wakefield et al., 2015). Although I did not have access to complete histories, in the multiple years that many individuals were tracked, some birds never left the south Atlantic Ocean, suggesting that there is no disadvantage to remaining in a productive region close to the colony and not exploring further. Indeed, the gradual increase in fidelity suggests that it is driven by familiarity to geographic spaces rather than a preference for a particular habitat, however habitat preference models are required to disentangle the two processes (Piper, 2011; Wakefield et al., 2015). Some birds repeatedly used certain regions at particular times of the year, which suggests they may target predictable aggregations of prey, such as the spawning events of cephalopods (Battam et al., 2010). Familiarity depends on the capacity to learn and remember physical and biotic features about an inhabited space (Cain et al., 1994; Brown et al., 2008), and in seabirds, which are extremely long-lived, memory is likely to be important (Regular et al., 2013).

During immaturity, shifts in distribution were less marked, yet this period may be prolonged as animals take time to develop an annual routine that enables them to recruit into the breeding population. Birds advanced their return date at the colony by around a week each year until they coincided with the average arrival date of adults, in line with previous results (Pickering, 1989). Overall, these results emphasize that decisions as a juvenile play an important role in determining lifetime distributions, and that environmental conditions experienced during development may have far-reaching consequences (Dall et al., 2012). It remains unclear from this study whether birds become more site-faithful as non-breeding adults, but it seems likely to be the case given the evidence for high fidelity in many other pelagic seabirds (e.g. Fayet et al., 2016b). Indeed, the general trend for long-term fidelity to particular regions suggests that pelagic seabirds might struggle to adapt to rapid change in the Southern Ocean (Grémillet and Charmantier, 2010). However, some birds did exhibit plasticity in foraging strategies in some years, and others showed little consistency; and it may be that climate change favours individuals that are more plastic in their movement and

foraging strategies (Charmantier et al. 2008). Incidental mortality in longline fisheries is a major source of mortality for wandering albatrosses from South Georgia, and juvenile birds are thought to be at highest risk due to their extensive overlap with pelagic longline tuna fleets (Phillips et al. 2016). Indeed, the selection of sites as juveniles may greatly influence lifetime mortality risk if preferred areas included high levels of fishing activity.

6.4.2 Ontogeny of at-sea behaviour

In their first few months post-fledging, the tracked albatrosses gradually increased their flight and foraging activity, particularly during daylight hours, likely associated with the development of flying skills, greater proficiency in prey detection and handling, and the optimal use of winds (Yoda et al., 2004; Riotte-Lambert and Weimerskirch, 2013). Flight and foraging activity peaked at around five months post-fledging, as individuals gained experience and physical maturity (Yoda et al., 2004; Daunt et al., 2007b). Riotte-Lambert and Weimerskirch (2013) also found that juvenile albatrosses from Crozet increase their flight activity over their first five months; however, due to the shorter tracking duration, they did not detect the decline in flight and foraging activity after about six months at sea, which subsequently follows a linear trajectory throughout immaturity. As the activity metrics are only proxies of foraging effort, they do not provide information on foraging success; however, as energy requirements are unlikely to decrease linearly over early life, it should be assumed that decreases in effort are a sign that birds are becoming more efficient at foraging, through increased knowledge of potential prey aggregations, or improved prey handling ability (Irons 1998). Indeed, these results are in accordance with Chapter 5, where I found a linear decline in foraging but not flight activity from early to late adulthood, and confirm the assumption that the immature period of seabirds is protracted due to a long period of learning of how to forage (Ashmole, 1963; Forslund and Pärt, 1995; Irons, 1998). The results presented here also verify that differences with age are caused, at least to some extent, by long-term within-individual improvements; however, it should be noted that this does not rule out the selective disappearance of less efficient foragers, which may also affect age-related differences in foraging strategies detected by cross-sectional studies (Forslund and Pärt, 1995).

6.4.3 Conclusions

Using longitudinal movement data for individuals tracked as juveniles up to adulthood, I demonstrate empirically that the ontogeny of foraging site selection and behaviour in albatrosses follows a consistent trajectory over a period of many years from fledging to recruitment. This study provides strong evidence that individuals gradually improve their foraging proficiency with age and emphasizes the role of individual experience in shaping long-term migration strategies. Furthermore, while it is well-known that the first few months at sea is a critical time when poor foraging ability can be a direct cause of mortality in seabirds (e.g. Daunt et al., 2007b), the results presented here also indicate that the movement patterns of juveniles play an important role in generating differences between individuals that are likely to be maintained throughout life, with potential implications for the population dynamics and conservation of this and other wide-ranging marine predators.

6.5 Abstract

Little is known about the ontogeny of habitat selection and foraging behaviour in animals with dispersive juvenile life stages, because of the challenges of tracking individuals over long time periods. In many pelagic species, the high incidence of foraging site fidelity in adults suggests that site selection is canalized over long periods of immaturity, yet this remains untested. I used a longitudinal tracking dataset from wandering albatrosses *Diomedea exulans* tracked over a 13-year period to investigate the ontogeny of foraging site selection and foraging behaviour. Individuals from the same cohort were tracked with geolocator-immersion loggers over multiple years from fledging, to the first season after recruitment into the breeding population. In the first few months after fledging, birds increased their flight and foraging activity and travelled northwards into subtropical waters, after which birds dispersed into all basins of the Southern Ocean. In their second year at-sea, individuals reduced the size of core areas, suggesting that birds had already located suitable foraging areas. Over the course of their early lives, there was a linear decrease in foraging effort and flight activity, and an increase in foraging site fidelity, indicating that the ontogeny of foraging behaviour and site selection follows a consistent trajectory over a period of many years from fledging to recruitment. By the immature period, the majority of individuals were consistent, many of them using foraging areas visited in their first year, suggesting that site familiarity plays an important role in shaping long-term movement strategies. As such, I propose that the movement patterns of juveniles play an important role in generating differences between individuals that are likely to be maintained throughout life, with potential implications for the population dynamics and conservation of this and other wide-ranging marine predators.

6. The ontogeny of foraging and migration strategies

7 GENERAL DISCUSSION

A fundamental goal for ecologists is to understand the drivers of animal movements, and their consequences for fitness. Moreover, understanding the processes that give rise to spatial patterns is integral to predicting how animals might encounter, and respond to anthropogenic threats. Pelagic seabirds are appealing study species for examining the links among individual traits, environmental drivers, movements and foraging behaviour, and population dynamics, as they tend to have extreme foraging and breeding strategies, are relatively easy to monitor, and integrate resources over vast spatial scales. For management purposes, the study of their spatial ecology is crucial for understanding and diagnosing the drivers of population trends, particularly as many species are declining, and the potential threats are dispersed in nature and span national and international jurisdictions. In this thesis, I focus predominantly on the drivers of variation in the movement and foraging strategies of seabirds during the non-breeding season, when they are no longer constrained to return to the colony at regular intervals to incubate the egg or provision young. I find that foraging strategies and habitat preferences are influenced by resource availability (Chapters 3, 4) and that differences in the distributions of birds between populations are driven by contrasting habitat preferences as well as intra-specific competition (Chapter 3). Also, intrinsic factors such as population of origin, sex, previous breeding outcome and age, as well as individual experience, can drive divergent movement and foraging strategies or habitat use (Chapters 2-6), which can influence fitness (Chapter 5). In this chapter, I discuss the extrinsic and intrinsic sources of variation investigated in the previous chapters of this thesis and their ecological implications. I then summarize the implications of this work for the applied management and conservation

of this threatened group of species. I finish by suggesting future directions for the rapidly advancing field of movement ecology.

7.1 The drivers and ecological consequences of variation in foraging strategies

7.1.1 Extrinsic drivers

The foraging and movement strategies of individuals are inherently linked to their environment (MacArthur and Pianka, 1966). Indeed, the availability of prey influences resource partitioning by predators (i.e. ecological opportunity; Araújo et al., 2011) and in environments with high variability in resources, animals are expected to be foraging generalists (Pianka, 2000). In the Southern Ocean, there is large seasonality in abiotic conditions throughout the year, which influences the availability and suitability of habitat. Specifically, seasonal sea-ice advance and retreat alters the area of ocean over which flying seabirds can forage, and drives latitudinal shifts in sea surface temperatures which influences the abundance and distribution of Antarctic krill *Euphasia superba* (hereafter krill) and other prey (Murphy et al., 2007). Accordingly, I found that the habitat preferences of non-breeding grey-headed albatrosses *Thalassarche chrysosto*ma differed substantially between winter and summer (Chapter 3). The preferences of birds from the Prince Edward Islands exhibited less seasonality than those from South Georgia, due to more benign conditions in the southwest Indian Ocean compared to the southwest Atlantic Ocean. In summer, albatrosses (particularly those from South Georgia) were more likely to use neritic regions associated with abundant resources such as krill (Xavier et al., 2003b; Atkinson et al., 2008), whereas in winter they relied more on largely predictable features in oceanic regions such as fronts and areas of high eddy activity (Nel et al., 2001; Scales et al., 2016).

In contrast to polar regions, tropical and subtropical environments generally have low primary productivity and resources are considered to be more patchily distributed (Ashmole, 1971). Many tropical species have been selected for high flight proficiency, enabling them to travel over vast oceanic areas searching for prey (Spear and Ainley, 1998; Ballance and Pitman, 1999; Weimerskirch et al., 2016). Murphy's petrels *Pterodroma ultima* travel immense distances - almost 5,000 km from their colony - during incubation trips (Chapter 4). Birds target two regions at the southern and eastern edges of the South Pacific Gyre, likely

because these areas are associated with more predictable and productive frontal regions than waters surrounding the colony. In order to travel such long distances, they spend around 95% of their time at sea in flight and appear to take advantage of trade winds to reduce flight costs. The selection for an extreme foraging behaviour, which results in the partner fasting on the nest for 20+ days (Brooke, 1995), enables them to live in one of the least productive marine regions on Earth (Claustre and Maritorena, 2003), where competition for foraging areas is likely to be lower than more productive regions along the equator (Ballance et al., 1997; Rayner et al., 2016).

During the breeding season, when birds are constrained to return to the colony, their foraging strategies will depend on the number of conspecifics with which they compete (Wakefield et al., 2013), and resources can be limiting due to prey depletion around breeding sites (Lewis et al., 2001; Wakefield et al., 2014). When no longer under the energetic and time constraints imposed by breeding, individuals are expected to select habitats that best reflect their intrinsic preferences (Cherel et al., 2007). In some species, individuals from different populations migrate across ocean basins and mix in extremely productive and predictable continental-shelf and upwelling habitats (González-Solís et al., 2007; Catry et al., 2011a). Grey-headed albatrosses disperse across the Southern Ocean, yet birds from different populations used contrasting regions, largely driven by divergent habitat preferences (Chapter 3). Population-specific preferences for particular habitats were similar to those used during the breeding season (Nel et al., 2001; Catry et al., 2004). Along with previous studies, these results suggest that allopatric populations may become specialized on habitats around the breeding colony, and if these differ between colonies, spatial segregation may persist during during non-breeding (Monteiro and Furness, 1998; Rayner et al., 2011). Additionally, by returning close to the breeding colony during what is ostensibly the sabbatical summer in this largely biennial species, some individuals may obtain additional mating opportunities (Ryan et al., 2007; Weimerskirch et al., 2015); moreover recent analyses suggest that non-breeders which regularly attend the colony have higher survival and breeding success (BAS, unpublished data).

It is likely that outside the breeding season, the sharing or partitioning of environmental or geographic space between populations is related to species-specific movement costs and resource availability. Many species of shearwaters are presumably able to coexist as they target superabundant resources, promoting dense aggregations of birds such as those in the

California Current (Shaffer et al., 2006; Ainley et al., 2009). In contrast, penguins have relatively high movement costs, giving them fewer productive habitats to move into and so they appear to partition resources along geographic or habitat boundaries (Thiebot et al., 2011a, 2012; Ratcliffe et al., 2014). As grey-headed albatrosses have low movement costs, yet do not target the most productive environments (Catry et al., 2004), it is likely that populations are able to coexist because individuals adopt a generalist strategy, partitioning geographic space at the population level across ocean basin scales (Chapter 3). Spatial segregation during the non-breeding season may be more widespread than previously anticipated. For example, there is increasing evidence that different species of gadfly petrels use largely non-overlapping regions (Chapter 4; Rayner et al., 2012, 2016). Also, black-browed albatrosses and white-chinned petrels from different populations appear to target distinct shelf or upwelling regions, potentially to avoid competition, but this requires further investigation (Grémillet et al., 2000; Phillips et al., 2005, 2006; Péron et al., 2010). For the purposes of conservation, persistent spatial and habitat segregation among species and populations may impede our ability to protect biodiversity hotspots using site-based approaches (Myers et al., 2000; Lascelles et al., 2016)

7.1.2 Intrinsic drivers

Foraging strategies ultimately depend on the internal state of the individual (Dall et al., 2004), as well as its movement and navigational capabilities (Nathan et al., 2008). As populations contain phenotypically diverse animals with varying abilities or resource preferences, foraging strategies may differ according to morphology, age, sex, breeding status or physiology, and reflect learned skills and past experiences (Bolnick et al., 2003). Where morphological differences arise, such as those related to sexual size dimorphism, foraging strategies are expected to differ according to social dominance or niche divergence (Phillips et al., 2004a; Araújo et al., 2011). Indeed, many seabirds are sexually dimorphic and sex differences in the diet and distribution of seabirds is generally greater during the breeding than the non-breeding season, suggesting that differences in resource partitioning arise as a result of competition (Phillips et al., 2011). In contrast, tracking and stable isotope studies of Southern Ocean albatrosses indicate that at various stages of the annual cycle, females consistently forage further north than males (Chapters 3, 4; Jaeger et al., 2009; Phillips et al., 2009; Froy et al., 2015), which suggests that differences are likely attributed to niche divergence through the effects of wing-loading on flight performance rather than competition

(Shaffer et al., 2001a; Phillips et al., 2004a). It is important to note, however, that there was greater evidence of sexual segregation in wandering *Diomedea exulans* than grey-headed albatross (Chapter 3, 5). The difference between the two species is not explained well by the degree of sexual dimorphism; in both species, males are around 20% larger than females and differ to a similar degree in wing loading (Shaffer et al., 2001a; Phillips et al., 2004a). It may be that because wandering albatrosses have the greatest latitudinal range and widest habitat preferences of any albatross species, there is greater scope for spatial segregation.

There is increasing evidence that sex differences in foraging strategy are not necessarily linked to different morphology, as they also arise in monomorphic species (Lewis et al., 2002). Differences during the pre-laying exodus seem to be associated with reproductive role specialization; however, results differ among species (Chapter 4; Hedd et al., 2014; Pinet et al., 2012). For example, female sooty shearwaters *Ardenna grisea* travel to more productive waters in order to build resources for egg development, whereas males remain closer to the colony, providing more time for defending the burrow (Nisbet, 1997; Hedd et al., 2014). In contrast, male gadfly petrels *Pterodroma* spp. generally travel further to more productive regions, presumably in order to build up fat reserves for their long incubation shift (Chapter 4; Pinet et al., 2012). Sex differences in foraging strategies can be species- and site-specific and may be driven by a multitude of factors (Phillips et al., 2011); future studies that investigate the ontogeny of sex differences may be better placed to determine the ultimate drivers of foraging differences (Kernaléguen et al., 2016).

It is well documented that age shapes the reproductive output of long-lived species, with an increase in early years, followed by a plateau, and for many species a decline due to senescence (Clutton-Brock, 1988; Jones et al., 2008; Froy et al., 2013). While foraging performance is likely to play a key role in determining individual fitness (Stephens and Krebs, 1986; Forslund and Pärt, 1995; Daunt et al., 2007a), the relationship between age and foraging strategy is less well established. Young individuals generally have poorer foraging skills, and improve with experience (Chapter 6; Yoda et al., 2004; Daunt et al., 2007b). In seabirds, the long period of immaturity appears to be related to the requirement to learn how to forage effectively in an environment in which resources are patchily distributed (Chapter 6; Ashmole, 1963). Indeed, juvenile and immature albatrosses consistently forage in the same regions, and fidelity gradually increases with age, probably related to progressive learning of the physical and biological attributes of particular sites, including the timing and fine-scale

locations of prey aggregations (Chapter 6; Piper, 2011). Many individuals consistently used sites visited in their first year. As such the movements of juveniles may play an important role in generating differences between individuals that are maintained throughout life, with potential fitness consequences.

Increased foraging experience with age has been documented in a few cases (Zimmer et al., 2011; Vaillant et al., 2013), and in old age, increased experience may be masked by senescent declines in physiological or muscular function (MacNulty et al., 2009; Hassrick et al., 2013; Elliott et al., 2015). For example, older male albatrosses appear to take longer foraging trips during incubation or travel further than younger males (Catry et al., 2006; Lecomte et al., 2010), which can result in reproductive failure. However, while many studies document declines in fitness traits with old age, comparatively few investigate changes in foraging parameters with old age (reviewed in Table 5.1) and subsequently link them to fitness outcomes (but see Chapter 5; Jaeger et al., 2014) .

As processes occurring in different seasons are inextricably linked (Marra et al., 2015), those occurring during non-breeding may have an important influence on breeding events (Harrison et al., 2011). In long-lived seabirds, increased foraging activity at-sea has been linked to a decreased probability of breeding, later laying and lower breeding success in the following success (Daunt et al., 2006, 2014; Shoji et al., 2015). Indeed, older (20+ years) non-breeding wandering albatrosses with higher foraging activity during non-breeding are more likely to defer breeding or fail to incubate an egg, but high foraging activity had no effect on reproductive performance in young birds (Chapter 5). These results suggest that older individuals pay a price if they expend greater effort, which is unexpected given the declining trend in number of landings over the lifetime of the wandering albatross demonstrated by both longitudinal and cross-sectional tracking samples of birds (Fig. 7.1; Chapters 5, 6).

Both foraging effort during non-breeding and breeding success experience a decrease with age, yet, surprisingly, reduced foraging effort does not predict lower breeding success (Fig. 7.1; Chapter 5). This suggests that declines in effort may be accompanied by an increased in foraging success, as hypothesized in Figure 7.1; however this does not explain reproductive senescence. Measuring foraging success across the lifetime would be crucial for determining if declines in foraging effort are due to the reduced ability to catch prey as a result of muscular function or reduced visual acuity (MacNulty et al., 2009; Lecomte et al., 2010), or are the product of increased experience. I hypothesize that foraging success increases during

early life and stabilizes during immaturity, but follows a gradual increase throughout adulthood (Weimerskirch, 1992; Weimerskirch et al., 2005). Future studies that specifically record the foraging activity, success (e.g. using stomach temperature sensors) and physiology of birds that experience senescent declines are required, in order to determine the fine-scale behavioural drivers of poor breeding success. Ultimately, longitudinal studies are crucial for disentangling the effects of age, environmental stochasticity and intrinsic quality (Daunt et al., 2014) .

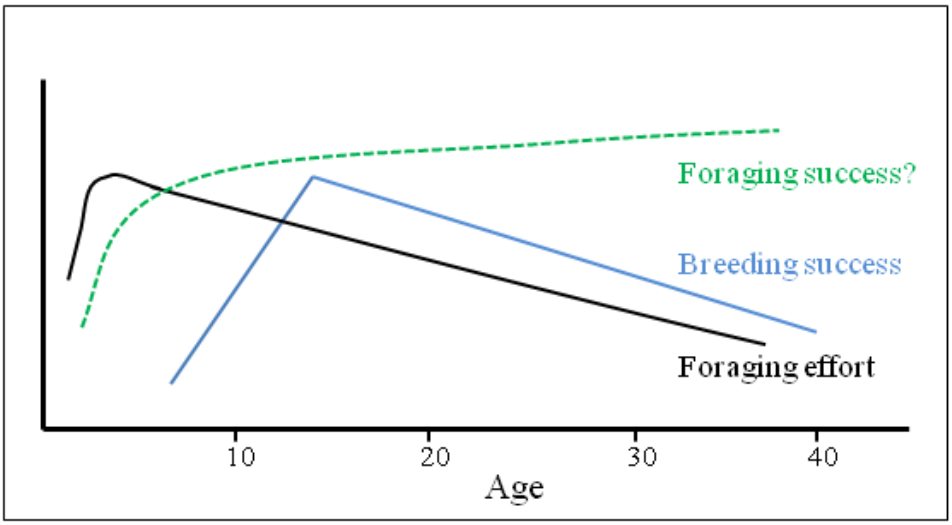


Figure 7.1. The relationship between age, breeding success (from Froy et al. 2013), foraging effort during the non-breeding season (landing rate during daylight; Chapters 5, 6) and foraging success (hypothesized relationship).

7.2 The conservation implications of variation in foraging strategies

The field of movement ecology is advancing rapidly, and tracking data are increasingly important for identifying key habitats for potential designation as marine protected areas (Maxwell et al., 2011; Lascelles et al., 2016). However, little attention has been paid to how many tracked individuals are required in order to gain population-level inference (but see Soanes et al., 2013), particularly during the non-breeding season, when individuals may disperse across ocean basins (Croxall et al., 2005; Chapters 3, 5). In Chapter 2, I quantified minimum sample sizes required to predict important areas for populations using data from 10 species of pelagic seabirds, encompassing a wide range of movement strategies. I found that the numbers of individuals needed to adequately represent core and general use areas were relatively modest, ranging from 3 to 22, and 10 to 27 individuals, respectively, depending on the species. As predicted, the minimum number required was directly linked to individual variability in movement strategies. For example, grey-headed and wandering albatrosses vary considerably in their use of non-breeding destinations and so require a larger tracking sample than black-browed albatrosses, which mostly migrate to the Benguela Upwelling. While these results are broadly applicable to many migratory species, future studies would ideally investigate the relationship between sample size and home range area for seabirds from other regions, such as transequatorial migrants with multiple winter destinations (e.g. Shaffer et al., 2006). Also, the greater smoothing of geolocator data likely results in greater overlap between individuals compared to finer-scale tracking (Soanes et al., 2013, 2015), so these results may not be applicable for studies using higher-resolution devices such as GPS or PTT. Nonetheless, appropriate sample sizes are critical if results from biologging studies are to be used for effective conservation, as quantification of overlap with threats and the identification of suitable habitats for designation as protected areas both rely on the assumption that within-population variation in movement strategies is well represented (Hays et al., 2016).

There is increased emphasis on the use of habitat models to predict the distributions of poorly known populations; however recent studies show that models may have poor transferability (e.g. Torres et al., 2015; Chapter 3). Predictive models are usually tested within the same temporal or spatial range, rather than extrapolated to novel areas (e.g. Louzao et al., 2006). While I did not explicitly map extrapolated predictions, the low performance scores of models tested on tracking data from the other population indicated that they did not predict distributions well. The models did, however, predict suitable habitat around colonies that

were not sampled, including in New Zealand, suggesting that birds from other breeding populations are likely to use these areas. Contrasting habitat preferences between populations and flexible preferences between seasons will influence the utility of real-time predictions from habitat models as a management tool (e.g. Hazen et al., 2016). The incorporation of multiple statistical approaches (e.g. ensemble niche modelling; Scales et al., 2016) will no doubt improve the accuracy of habitat models; yet for species with broad habitat preferences such as albatrosses and petrels, the collection of tracking data from unsampled sites is still recommended, where logistically and financially possible.

The greatest threat for many species of albatrosses and petrels remains incidental mortality (bycatch) in industrial longline and trawl fisheries (Phillips et al., 2016). In particular, declines of albatrosses from South Georgia have been attributed to mortality of adults and juveniles in pelagic longline fisheries, and for grey-headed albatrosses, climate variability has also reduced adult survival (BAS, unpublished data). While I did not conduct an analysis of overlap between birds and fishing vessels, the distribution of juvenile and adult female wandering albatrosses in relation to males (Chapters 5, 6) explains the sex- but not age-biased bycatch in longline fisheries, particularly in the southwest Atlantic Ocean (Croxall and Prince, 1990; Jiménez et al., 2016; Gianuca et al., 2017). In contrast, grey-headed albatrosses are predominantly caught by longline vessels in the Indian Ocean (Nel et al., 2002), and so the contrasting population trends of birds from South Georgia and the Prince Edward Islands are not explained well by spatial overlap of non-breeding adults with fishing vessels (Chapter 3). Little is known about the distribution of juvenile and immature birds and this information is crucial for understanding the causes of declines. Moreover, the fidelity of young wandering albatrosses to particular regions suggests that some individuals are likely to experience much greater overlap with fishing vessels over the course of their lives (Chapter 6); however, their risk of mortality also depends on finer-scale interactions with vessels such as the likelihood of attendance and reliance on discards (Granadeiro et al., 2011).

7.3 Future directions

Some of the chapters in this thesis benefited greatly from longitudinal tracking data and breeding histories of the same individuals over many years. With the increasing ability to follow the behaviours of wild animals over extended time periods, there is growing interest in the mechanisms driving individual variation in movements and behaviours (Dall et al., 2004; Kays et al., 2015) and their implications for lifetime reproductive success (Clutton-Brock and Sheldon, 2010; Senner et al., 2015). The results from Chapter 6 raise new and exciting questions regarding the evolution and maintenance of particular foraging and migration strategies, and in the following section, I have selected two promising research directions.

The drivers of juvenile movements and foraging strategies

The work in this thesis revealed that among and within populations, individuals exhibit strikingly different patterns of movement. It may be that a large proportion of phenotypic variance in movement traits is genetic (Liedvogel et al., 2011), and studies of migratory traits in songbirds have revealed considerable additive genetic variation for single traits (e.g. timing of migration; Pulido et al., 2001). There is limited knowledge of the relative roles of innate and environmental factors in the movement and dispersal strategies of juvenile seabirds. However, as demonstrated in Chapter 6, there can be large variability between individuals even within the first few months, and site selection is repeatable, suggesting a heritable component. Nonetheless, estimating the additive genetic component of a trait such as migration strategy, whilst controlling for confounding effects such as dominance, common environment or parental effects, requires a large pedigree consisting of individuals from multiple generations (Wilson et al., 2010). Tracking datasets may soon be comprehensive enough to test this fully; in the meantime, parent-offspring studies may still provide insights into whether related individuals have movement strategies that are more similar than expected by chance. Another avenue for research could be to determine the role of local wind patterns in promoting variation between individuals in the first year, by simulating wind-assisted dispersal over a range of years and for birds from different populations, and comparing these results to observed patterns, as in other species (Hays et al., 2010; Scott et al., 2014).

7. Discussion.

The demographic consequences of individual foraging strategies

Individual specialization, whereby individuals use a small subset of the population's available resources is widespread (Bolnick et al., 2003; Araújo et al., 2011), yet the ecological implications remain unclear as few studies document an advantage in terms of fitness (Votier et al., 2004; Woo et al., 2008; but see Authier et al., 2012). Despite this, recent evidence suggests that individual variability in early life fitness traits, such as the age at first reproduction, can be an important predictor of lifetime reproductive output (Reed et al., 2003; Fay et al., 2016). As such, individual variability in resource use or foraging ability during early life may have an important role in determining lifetime fitness. In this thesis, because a relatively small sample of individuals were tracked repeatedly across the immature period, I could not reliably link particular movement and foraging strategies to fitness measures, such as the age of first reproduction. Future studies that are able to collect longitudinal tracking and breeding information from a demographically informative sample of individuals should be better placed to explore the links among resource selection and specialization, foraging site fidelity and fitness across the lifespan (Gaillard et al., 2010). As seabirds take many years to mature and are usually long-lived, other species, such as terrestrial migrants, may be more suitable subjects with which to explore lifetime movements (Dingle, 1996; Kays et al., 2015). Furthermore, fine-scale information on the energy expenditure of individuals is increasingly accessible (i.e. through accelerometry), enabling the quantification of movement and foraging costs of particular strategies (e.g. Flack et al., 2016). Such datasets, in combination with demographic models, will enable researchers to determine the evolutionary and ecological consequences of particular strategies in the context of rapid environmental change (Teitelbaum et al., 2016).

7. Discussion.

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8. References

9 APPENDICES

9. Appendices

APPENDIX 1 – SUPPLEMENTARY MATERIAL FOR CHAPTER 2

Methods

Deployment details

Geolocator-immersion loggers (Mk3-5, Mk7; British Antarctic Survey, Cambridge, UK) were deployed on the tarsus of adult wandering albatrosses between February 2003 and January 2009 and retrieved between November 2004 and January 2011, as part of a long-term tracking program. These data correspond to three sabbatical years (2004, 2008 and 2009) for previously successful breeders. Geolocators (Mk3) were also deployed on 26 light-mantled sooty albatrosses (LMSA) in December 2003 and retrieved between one and five years later. Logger battery failure resulted in reduced sample sizes for the later years, and only the first two years of data are included here, providing a sample of 25 and 11 birds for 2004 and 2005, respectively. LMSA are not monitored routinely at their nesting sites and breeding status was inferred from a combination of longitudinal movements and activity patterns. Incubation shifts were detected from extended periods of dry activity data of *c.* 10+ days in late October to early January (Weimerskirch and Robertson, 1994). Whilst LMSA breed biennially if successful, all individuals appeared to fail during incubation or chick-rearing in summer 2003/04 and returned to the colony the following breeding season (2004/05). As a result, I consider the 2004 and 2005 tracking periods as separate non-breeding seasons. I pooled the 11 birds tracked over 2005, 7 and 4 of which appeared to defer breeding and fail during early incubation, respectively, as they departed the colony at similar times.

Details on predicting minimum sample sizes

I conducted a sensitivity analysis to evaluate the performance of four non-linear models. The models were run using the *drc* package in R (Ritz and Strebig, 2015), originally designed for enzyme dose-response curves, and are specified below.

3-parameter Michaelis-Menten:

$$y = c + \left(\frac{a - c}{b + x}\right) x$$

where c = the value of the y axis when $x = 0$, a = the asymptotic value of the y axis, and b = the value of x at which the y value is halfway between a and c. The two-parameter Michaelis-Menten is obtained by setting $c = 0$, giving the following:

2-parameter Michaelis-Menten:

$$y = \frac{ax}{(b + x)}$$

3-parameter asymptotic exponential:

$$y = a - be^{-cx}$$

For the 2-parameter version, $a = b$, giving us the following equation:

2-parameter asymptotic exponential:

$$y = a(1 - e^{-cx})$$

Information on how I extrapolated the minimum number of individuals to track from asymptotic models is given in Figure A1.1. Extrapolations were made separately for the modelled curve and upper and lower 95% confidence intervals. I also tested whether predictions from models were sensitive to the number of resampling iterations, comparing 1,000 and 10,000 iterations. As predictions based on 1,000 or 10,000 iterations were significantly correlated for both population core (Pearson's correlation, $R = 0.99$, $P < 0.001$) and general use areas (Pearson's correlation, $R = 0.99$, $P = < 0.001$), I used 1,000 resampling iterations for all analysis in this chapter to minimise computational demands.

Sub-sampling procedure

I carried out a sub-sampling procedure to test for the effect of individual consistency, the number of individuals tracked and the chance selection of individual movement strategies within my samples. From the year with the larger sample, I took a random sample of individuals to match the sample size of the other year and predicted the minimum sample sizes required. For AP, LMSA and WA where the sample of individuals in one year (Yr_1) was repeated as part of a larger sample in another year (Yr_2), I created two sub-samples from the larger year (such that $n = Yr_1$); a random sample of individuals including all repeated individuals, and one without any repeated individual. I resampled these samples and

predicted sample sizes for both $n = Yr_1$ and $n = Yr_2$ to determine if differences were due to sampling of individuals or sample sizes. For BBA, as all individuals ($n = 24$) were tracked in both years, I sub-sampled two sets of repeated individuals ($n = 12$) and compared predictions between the sub-samples and between years. Finally, no BS were tracked for more than one year, so to compare sampling differences between years, I randomly sub-sampled 6 individuals tracked in 2012 and compared predictions with the larger 2012 sample and with birds tracked in 2002 (See Table A1.4 for more details).

Results

Sub-sampling procedure

By sub-sampling datasets, it was apparent that differences among years were also influenced by the chance selection of individuals in the sample and the size of the sample, depending on the species (Table A1.4). For LMSA, predictions appeared to vary little as a result of sub-sampling, whereas for AP, the larger minimum sample size for core areas in 2011 appeared to be driven by one individual which migrated to a different ocean basin (Fig. 2.3b), rather than by the smaller sample size (Table A1.4). For BS, sub-sampling of the larger 2012 sample reduced minimum sample sizes to levels similar to those for the 2002 sample, suggesting that the variation resulted largely from the difference in original sample sizes. For BBA, predictions were sensitive to the selection of individuals within the tracking sample, as both sub-sampled datasets for 2002 and 2003 differed substantially and the contrast was greater than that between years (Table A1.4). Finally, WA tracked in 2004 and 2008 were more variable in their migration strategies than in 2009 (Fig 2.3); differences did not appear to be driven by the lower sample size, as predictions were substantially lower than for sub-samples of data from 2008 and 2009 (Table A1.4)

Table A1.1. AIC values of different models tested for core (50%) and general use (95%) areas as a function of sample size.

Species	Year	Core area				General use area			
		MM2	MM3	AR2	AR3	MM2	MM3	AR2	AR2
AP	2010	-11892.4	-11892.5	-11654.9	-11884.5	13156.7	13122.4	14158.2	13146.5
	2011	-4330.4	-4364.0	-4345.4	-4363.7	21291.5	21293.1	21348.5	21295.6
BBA	2002	9618.9	9480.2	9312.2	9285.1	133047.5	132843.4	134653.7	133079.9
	2003	7766.5	7680.2	7643.9	7598.1	123986.7	123923.4	125195.5	124109.5
BP	2011	18639.8	18638.3	18659.3	18637.2	45033.3	45017.5	45195.6	45018.7
BS	2002	-6236.8	-6266.1	-6191.4	-6256.3	6066.6	6068.5	6425.1	6069.1
	2012	16299.0	16142.3	16278.3	16171.1	69471.3	69451.6	70793.3	69763.4
GHA	1999-2000	53554.0	53543.4	54463.7	53642.6	140072.4	139712.1	142291.6	139897.2
LMSA	2004	18230.2	18111.2	19243.1	18285.7	112497.5	112426.6	114642.9	112675.7
	2005	951.3	949.6	1727.7	990.1	-554581.0	-554613.7	-553852.0	-553944.9
NGP	2000	-25089.2	-25149.4	-23539.4	-24923.4	37667.6	37419.8	43635.0	38025.0
SGP	2000	1910.4	1900.8	1941.5	1893.0	123600.8	123571.7	125380.6	123798.3
WA	2004	40173.4	40168.6	40867.7	40171.6	86099.6	86079.9	87715.6	86275.4
	2008	100870.7	100820.6	102064.4	101194.4	195578.8	195485.5	205377.8	197959.2
	2009	78868.2	78839.7	79759.4	78902.3	204378.7	204133.2	208200.8	204866.3
WCP	2003	102.9	32.3	117.7	63.1	23389.4	23355.0	24226.5	23411.1

For each-species combination, the best supported model (with the lowest AIC) is highlighted in bold. AP = Antarctic prion, BBA = black-browed albatross, BP = blue petrel, BS = brown skua, GHA = grey-headed albatross, LMSA = light-mantled sooty albatross, NGP = northern giant petrel, SGP = southern giant petrel, WA = wandering albatross, WCP = white-chinned petrel

Table A1.2. Predicted minimum sample sizes for core (50%) and general use (95%) areas for projected 'colony' sizes of 50, 100 and 1,000 individuals.

Species	Year	Sample size	Core area			General use area		
			50	100	1,000	50	100	1,000
AP	2010	9	6 (6 – 7)	7 (6 – 7)	7 (7 – 8)	12 (11 – 13)	14 (13 – 14)	16 (14 – 17)
	2011	6	11 (10 – 12)	12 (11 – 13)	13 (12 – 15)	13 (10 – 15)	14 (11 – 17)	16 (12 – 20)
BBA	2002	25	7 (7 – 7)	7 (7 – 7)	7 (7 – 7)	27 (26 – 27)	37 (36 – 38)	57 (55 – 60)
	2003	24	6 (6 – 6)	6 (6 – 6)	7 (7 – 7)	21 (21 – 22)	26 (27 – 28)	36 (35 – 38)
BP	2011	9	5 (3 – 9)	5 (3 – 11)	6 (3 – 12)	24 (23 – 25)	32 (29 – 34)	45 (40 – 49)
BS	2002	6	11 (10 – 11)	12 (11 – 13)	13 (12 – 14)	12 (11 – 12)	13 (12 – 14)	15 (14 – 16)
	2012	19	14 (13 – 14)	16 (15 – 16)	18 (17 – 19)	23 (23 – 23)	30 (29 – 31)	42 (40 – 43)
GHA	1999-2000	22	16 (15 – 16)	19 (18 – 19)	22 (22 – 23)	26 (25 – 26)	35 (34 – 36)	53 (51 – 55)
LMSA	2004	27	8 (8 – 8)	9 (9 – 9)	9 (9 – 9)	16 (16 – 17)	19 (19 – 20)	24 (23 – 25)
	2005	11	7 (7 – 8)	8 (7 – 8)	8 (8 – 9)	15 (14 – 16)	18 (17 – 19)	21 (20 – 23)
NGP	2000	25	7 (7 – 7)	8 (8 – 8)	8 (8 – 9)	10 (10 – 10)	11 (11 – 11)	12 (12 – 12)
SGP	2000	29	3 (3 – 4)	4 (4 – 4)	4 (4 – 4)	16 (16 – 16)	19 (18 – 19)	23 (22 – 23)
WA	2004	15	22 (22 – 22)	28 (28 – 29)	39 (37 – 40)	21 (21 – 22)	27 (27 – 28)	37 (35 – 38)
	2008	37	18 (18 – 18)	22 (21 – 22)	27 (26 – 27)	23 (23 – 23)	30 (30 – 30)	41 (41 – 42)
	2009	33	14 (14 – 14)	16 (16 – 16)	19 (18 – 19)	26 (26 – 27)	36 (36 – 37)	55 (54 – 55)
WCP	2003	10	14 (14 – 15)	17 (16 – 18)	20 (19 – 21)	19 (18 – 19)	23 (22 – 24)	29 (28 – 31)

Values are shown with 95% confidence intervals in parentheses. AP = Antarctic prion, BBA = black-browed albatross, BP = blue petrel, BS = brown skua, GHA = grey-headed albatross, LMSA = light-

mantled sooty albatross, NGP = northern giant petrel, SGP = southern giant petrel, WA = wandering albatross, WCP = white-chinned petrel

Table A1.3. Summary of the best five supported GLMM testing the effects of individual variability, the log of population area (*Pop. area*), sample size (*Sample*), and the interaction between the latter two on the predicted sample required to represent core (50%) and general use (95%) utilization distributions (UDs) of the population for each species-year combination.

Pop. area	Sample	Individual variability	Pop. area: Sample	d.f.	AICc	ΔAICc	AICcW
Core area							
X	–	X	–	5	85.9	0.00	0.62
X	X	X	–	6	87.1	1.28	0.32
X	X	–	–	5	92.9	7.01	0.02
–	–	X	–	4	93.0	7.18	0.02
X	X	X	X	7	93.8	7.93	0.01
General use area							
–	–	X	–	4	92.4	0.00	0.52
X	–	X	–	5	93.3	0.93	0.33
–	X	X	–	5	95.8	3.43	0.09
X	–	–	–	4	98.2	5.81	0.03
X	X	X	–	6	98.7	6.26	0.02

X indicates predictors that were retained by the most parsimonious models, and – indicates predictors that were not retained in the analysis. AICc: Akaike information criterion correction for small sampl sizes; AICcW: the weight given to that model.

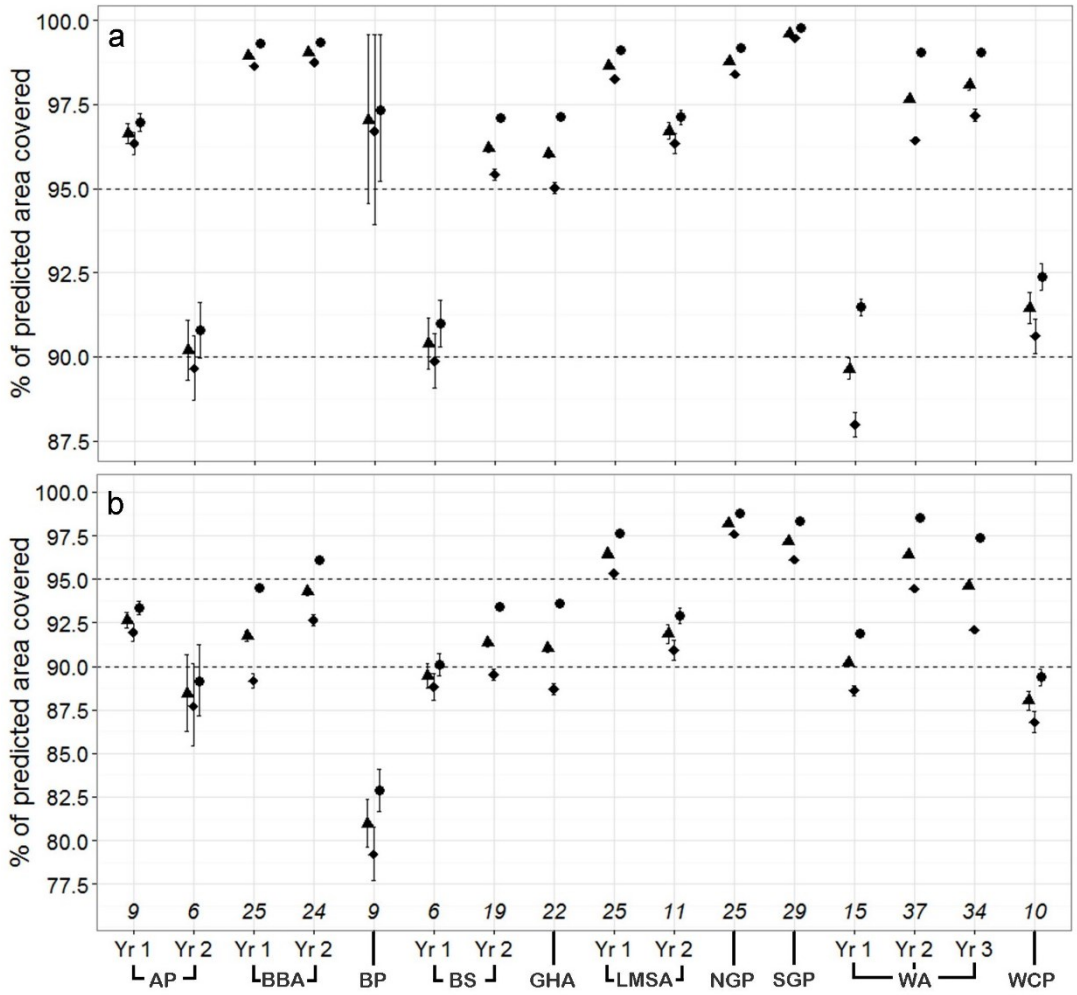


Figure A1.1. Percentage of predicted population a) core (50% UD) and b) general use (95% UD) area covered by tracking samples for each species-year combination (multiple years for the same species indicated as Yr1 - Yr3). Predictions are shown with confidence intervals, where large enough to be visible, and have been made for a projected 'colony' size of 50 (circles), 100 (triangles) and 1,000 (diamonds) individuals. Sample sizes for each group are indicated at the bottom of the plot and dashed horizontal lines indicate 90% and 95% cut-offs.

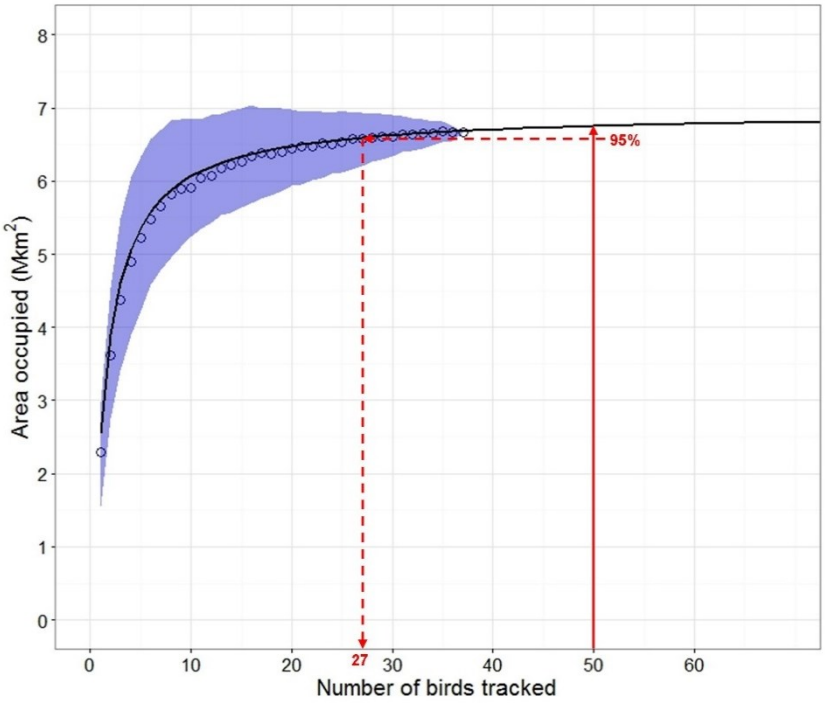


Figure A1.2. Schematic of the process used to predict minimum sample size for a projected population size, in this case 50 individuals, for wandering albatrosses tracked in 2008. The predicted sample size is the x-value for which the y-value equals 95% of the area occupied at x = 50, in this case, 27 individuals. The 95% confidence intervals (CIs) around predicted samples are calculated in the same way as for the CIs around the modelled curve.

Table A1.4. The effects of sample size (n) and chance selection of sampled individuals on predicted minimum sample sizes (Sample) for each species tracked in more than one year (Sp. + year). For each species, sub-sampling was performed on the larger sample of the two years (under Reduced sample) to obtain one sub-sample containing individuals tracked twice (Repeats retained) and another without those individuals (Repeats removed). Results are shown for core (50%) and general use (95%) utilization distributions (UDs). For each sub-sample, predictions for the full sample are given (Full sample), as are predictions for the other year for that species (Other year).

Sp. + year	UD	Reduced sample				Full sample		Other year	
		Repeats removed		Repeats retained					
		Sample	n	Sample	n	Sample	n	Sample	n
AP 2011	50	7 (6 – 7)	6	7 (6 – 7)	6	6 (6 – 7)	9	11 (10 – 12)	6
	95	14 (13 – 15)	6	10 (9 – 11)	6	12 (11 – 13)	9	13 (10 – 15)	6
BS 2012	50	11 (11 – 12)*	6	–	–	14 (13 – 14)	19	11 (10 – 11)	6
	95	17 (16 – 18)*	6	–	–	23 (23 – 23)	19	12 (11 – 12)	6
BBA 2002	50	14 (13 – 15)[v]	12	4 (4 – 4)	12	7 (7 – 7)	25	–	–
	95	29 (28 – 30)[v]	12	14 (14 –15)	12	27 (26 – 27)	25	–	–
BBA 2003	50	8 (7 – 8)[v]	12	6 (6 – 7)	12	6 (6 – 6)	24	–	–
	95	23 (22 – 25)[v]	12	14 (14 – 15)	12	21 (21 – 22)	24	–	–
LMSA 2004	50	8 (8 – 9)	11	9 (9 – 9)	11	8 (8 – 8)	25	7 (7 – 8)	11
	95	7 (7 – 7)	11	12 (11 – 13)	11	9 (9 – 9)	25	9 (8 – 9)	11
WA 2008	50	16 (16 – 17)	15	21 (20 – 22)	15	18 (18 – 18)	37	22 (22 – 22)	15
	95	24 (23 – 24)	15	24 (24 – 24)	15	23 (23 – 23)	37	21 (21 – 22)	15
WA 2009	50	13 (13 – 14)	15	12 (12 – 13)	15	14 (14 – 14)	33	22 (22 – 22)	15
	95	25 (25 – 26)	15	24 (23 – 24)	15	26 (26 – 27)	33	21 (21 – 22)	15

** indicates that for BS there were no individuals tracked twice, so these values represent just the full year (2012) which was sub-sampled to enable comparison with 2002.* [v] *indicates that the BBA data in both years are from the same individuals.*

9. Appendices

APPENDIX 2 – SUPPLEMENTARY MATERIAL FOR CHAPTER 3

Methods

Deployment details and spatial analyses

Forty-seven geolocators (British Antarctic Survey, Cambridge, UK) were deployed on chick-rearing adults at Bird Island in April 1999, all of which fledged chicks. Loggers were retrieved and data downloaded from 22 loggers (from 6 males, 16 females) in September - November 2000 (Croxall et al., 2005). In November 1999, 29 loggers were deployed on adults, all of which failed during late incubation in December and January, and 19 were recovered the following breeding season (from 9 males, 5 females, 5 unsexed). On Marion Island, 20 and 18 geolocators were deployed in April 2002 and 2003, respectively, of which 14 and 11 devices were recovered in October 2003 and 2004, respectively (total 12 males, 12 females). All but one bird at PEI fledged a chick; data from this failed bird were excluded from analyses for sample size considerations.

For comparison of utilization distributions (UDs), I selected the 90% rather than the 95% contour to remove locations associated with transient migratory phases. The bootstrapping of sample size was for the 50% and 90% UDs and this was repeated for 1,000 iterations. It was assumed that when home-range area reached an asymptote, a sufficient number of individuals had been tracked. I ran a series of models to compare the non-breeding characteristics of birds from different groups. I compared the combined effect of population and sex for successful birds with generalized linear mixed-effects models (GLMMs) using the lme4 package in R (Bates et al., 2015). I used a Gaussian error structure for all models except one, where a binomial structure was used as the response was a proportion (percentage circumpolar trips). The random effect of year was included to control for potential differences between the two years of tracking data for PEI. I included sex, population and their two-way interaction as explanatory covariates and used backwards model selection to assess important variables. In all models, the interaction between sex and population was non-significant (*P*-values are not reported) (Table 3.2). I also carried out a similar procedure with breeding outcome for SG birds, using generalized linear models (GLMs) to test for the effects of sex, breeding outcome and their two-way interaction. *F*-test values are quoted for most characteristics, and a Chi-square test for the remainder (Table 3.3). None of the two-way

interactions between breeding outcome and sex or any of the sex effects were significant, thus only the influence of breeding outcome is shown (Table 3.3).

The null hypothesis of my randomization procedure was that there would be no difference in the spatial distribution of the two groups. If upheld, then the size of the overlap should not be significantly different from the size of the overlap if the composition of the groups were randomly assigned (Breed et al., 2006). I generated my null expectation by creating kernels from groups that had been assigned randomly using the same sample sizes as the original groups and calculated the overlap. I calculated randomizations 1000 times from the pooled dataset. *P*-values were determined by the proportion of random overlaps that were smaller than the observed overlap; i.e. if the observed overlap was less than all randomizations, then $P \leq 0.001$ (Breed et al., 2006). Firstly, I calculated spatial segregation for PEI birds from both tracking years to determine if the distributions were significantly different; this was not the case, and years were pooled for further analyses.

Habitat modelling

I modelled simulated movements for my null model in the form of correlated random walks (CRW) (Kareiva and Shigesada, 1983). Each CRW was assigned to a real bird track on a given date. I removed the first and last two weeks of the non-breeding season, which were likely to correspond with periods of directed, migratory movements, as these are more challenging to integrate into the CRW approach. I also restricted simulations to not occur over land, and to be confined within the range of all the locations, defined by the local convex hull non-parametric kernel (Getz et al., 2007). The range was expanded by a 200 km buffer to take into account the mean error of geolocation (Phillips et al., 2004b). Using methods similar to Žydelis et al., (2011), I tested the effects of different numbers of simulations on the performance of my models. I ran a set of models consisting of all observed tracks and varying numbers of simulations of up to 50 per individual (Žydelis et al., 2011). I found that both the χ^2 values for each parameter and the area under receiver operator curve (AUC) stabilized at about 20-30 simulations per individual (Fig. A2.6). Consequently, I chose 30 simulations per observed track for each of the models.

I sourced habitat variables from online databases (see Table A2.3). Ocean floor depth was sampled from the GEBCO bathymetric dataset (IOC 2003). Monthly composites of sea surface temperature (*SST*) and chlorophyll α concentrations (*Chl*) were extracted to avoid

data loss due to cloud cover. *SST* was downloaded from the NOAA Pathfinder Advanced Very High Resolution Radiometer (AVHRR) *v.5* dataset, *Chl* from the SeaWiFS sensor, made available from the Oceancolor website (http://oceancolor.gsfc.nasa.gov/). Both sea level anomaly (*SLA*) and eddy kinetic energy (*EKE*) were used as indicators of mesoscale turbulence (Wakefield et al., 2009a). I considered *EKE* as a measure of the intensity of mesoscale activity, and *SLA* as a measure of the eddy type (warm or cold). Eight-day *SLA* was taken from the Delayed-Time MLSA updated dataset and *EKE* was calculated from geostrophic current velocities. Both were extracted from Aviso (http://www.aviso.oceanobs.com/) via the Marine Geospatial Ecology Tools (MGET) extension in ArcGIS 10.1 (Roberts et al., 2010). Wind speed was downloaded from Ifremer (http://cersat.ifremer.fr/) at an 8-day temporal resolution. Up until August 1999, only ERS-2 gridded means were available, after which I used QuikSCAT gridded mean wind fields. I used the standard deviation of the values within each buffer as a measure of the gradient in bathymetry (*Depth std*) to represent shelf-edges or seamounts, and also for sea surface temperature (*SST std*) and productivity (*Chl std*) as GHA are known to target frontal systems (Nel et al., 2001; Waugh et al., 1999).

I investigated appropriate measures of competition and accessibility in the form of two groups of candidate predictor variables: 1) the projected distance from the population of origin and from the closest major population, and 2) this distance weighted by population size (Wakefield et al., 2011). Distances were calculated in the South Pole Lambert Azimuthal Equal Area projection in ArcGIS 10.1 using the *cost distance* function and were not allowed to cross land barriers. As both sets of distance and weighted distance variables were strongly correlated, I ran preliminary models containing either distance or weighted distance variables. In both cases, the distance variables produced models with lower AIC scores. Consequently, I consider the distance from the nearest major population as an indicator of avoidance due to competition, and the distance from population of origin as an indicator of potential avoidance of local birds or accessibility of a habitat, depending on the response. Major populations were considered to be island groups with >50 annual breeding pairs (Table A2.1).

To account for geolocation error (Phillips et al., 2004b), I created a 200 km buffer around each location and simulation, and extracted the mean value within each buffer. All records with incomplete environmental information e.g. due to cloud cover, were removed before analysis, which, for the complete dataset summed to around 20% of all records. I

standardized variables to improve the spread of the data and model convergence; *Chl* and *EKE* were log-transformed and *SST std* and *Depth std* were square root-transformed. I checked for correlation of predictor variables by calculating all pairwise Spearman rank correlation coefficients. When pairs of predictor variables were highly correlated (>0.6), I ran two models with each predictor and selected the model with the lowest Akaike Information Criteria (AIC) value (Burnham and Anderson, 2004). *Chl* and *Chl std* were highly correlated and so *Chl* was chosen as it resulted in greatest model fit.

The inclusion of a random intercept for individual ID can help control for variability in response to the environment (Aarts et al., 2008; Wood, 2006); however, model selection and inference in large datasets is computationally demanding within the mixed effects framework. Thus, I chose to use generalized additive models (GAMs), and tested the trained models on each individual, so that metrics of model performance took individual differences into account. When constructing GAMs, I initially set the maximum number of knots to 4 to reduce over-fitting and increased the number of knots only if the model response curves did not match the raw data. Also, to reduce over-parameterization, smoothers were produced using cubic regression splines with shrinkage which penalize variables during fitting (Wood, 2006). I checked for spatial autocorrelation of model residuals using semi-variograms in the Geo-R package in R (Diggle, 2015); this was not detected at the relevant spatial scale and was therefore deemed not to influence the results.

I ran all combinations of variables using the dredge function and ranked models according to AIC, and individually assessed the importance of each variable based on the proportion of deviance explained. For each term, I calculated the unique deviance explained by subtracting the deviance of the model excluding that term from the full model deviance. I also calculated the deviance shared with other predictors by subtracting this unique deviance from the amount explained by a model just with that term.

I created spatial predictions at the temporal scale of the underlying environmental data; monthly for *Chl, SST* and *SST std*, and weekly for the remaining dynamic variables. The environmental data were also resampled to match the spatial resolution of the original extractions. Weekly predictions of suitable habitat were scaled to 1 and summed over the season to produce spatial predictions for each population in summer and winter. I compared weekly AUC scores of the three predictor types using linear models, with AUC score as the response, and the week and predictor type (full, habitat or constraints) as covariates. If the

best model retained the predictor type, I concluded those drivers were better at explaining spatial patterns. I ran paired t-tests to determine if the inclusion of the sex or breeding outcome-specific smoother produced significantly different AUC scores. If significant, this confirmed that the relevant factor influenced habitat use.

Results

Migration characteristics

A greater proportion of birds from Prince Edward Islands (PEI) tended to perform circumpolar trips (83%) than South Georgia (SG) birds (52%) (GLMM: $X^2_1 = 3.5$, $P = 0.06$; Table 3.2); leading birds from PEI to range further from the colony (8,200 ± 1,200 km to 6,700 ± 2,900 km; GLMM: $X^2_1 = 4.4$, $P = 0.037$). Despite travelling further, the non-breeding period was shorter for PEI birds (GLMM: $X^2_1 = 8.6$, $P = 0.003$), principally because they returned 19 days earlier to the colony (GLMM: $X^2_1 = 9.9$, $P = 0.002$).

After breeding failure, SG birds (58%) travelled west to the southeast Pacific, and all but one of the remainder (37%) stayed in the local area (Fig. 3.2). One bird commenced a remarkable clockwise circumpolar trip, making a direct commute of over 18,000 km to the central Pacific in just over 17 days. During mid-summer, failed birds used southerly areas around the Bellingshausen Sea and then moved further north to the west coast of Chile during late-summer (Fig. 3.2). As a result, failed and successful birds were more segregated than expected by chance (observed overlap 1.01 and randomized overlap 1.45 ± 0.17, $P = 0.001$; Table 3.1). During winter, like the successful breeders, failed GHA that went east foraged in the southwest Indian Ocean, whereas local birds mainly foraged around the Falkland Islands with a few travelling to the Mid-Atlantic Ridge in late-winter (Fig. 3.2). As a result, there was no apparent spatial segregation from successful breeders during winter (observed overlap 1.71 and randomized overlap 1.63 ± 0.22, $P = 0.65$).

Table A2.1. Summary of global breeding populations of grey-headed albatrosses and their foraging ranges during breeding.

Population and abbreviation	Annual breeding population (pairs)	Latitude (°)	Distance and direction of PF from colony (km)	Mean max. foraging range (km)		Absolute max. foraging range (km)	
				Inc.	CR	Inc.	CR
South Georgia (SG)	47,674 [1]	-54.0	390 N	1372 [6]*	571 [6]*	-	1,760 [7]
Prince Edward Is. (PEI)	10,344 [2]	-46.8	337 SW	2182 ±1,408 [8]	722 ± 538 [8]	4,060 [8]	1,812 [8]
Crozet Is. (CRO)	5,940	-46.1	673 S	-	-	-	-
Kerguelen Is. (KER)	7,900 [3]	-49.4	191 N	-	-	-	-
Macquarie Is. (MAC)	94	-54.6	340 S	-	-	*c.* 2,100 [9]¥	-
Campbell Is. (CAM)	6,600 [4]	-52.5	857 S	-	1,567 ± 751 [10]	-	2,714 [10]
Diego Ramirez Is. (DR)	17,178 [5]	-56.5	366 S	-	-	*c.* 3,100 [11]¥	*c.*1,700 [11]¥

*1Poncet et al., 2006, 2Ryan et al., 2009, 3Weimerskirch et al., 1988, 4Moore, 2004, 5Robertson et al., 2007, 6Phillips et al., 2004a, 7Catry et al., 2004, 8Nel et al., 2000, 9Terauds et al., 2006, 10Waugh et al., 1999, 11Robertson et al., 2014. *Standard deviations not available as means calculated from averages. ¥ Values estimated from published figure of maximum foraging areas during breeding. PF = Polar Front, Inc. = incubation, CR = chick-rearing. Mean maximum foraging range represents the mean of individuals and absolute maximum represents the largest individual foraging range. Values are mean ± standard deviation.*

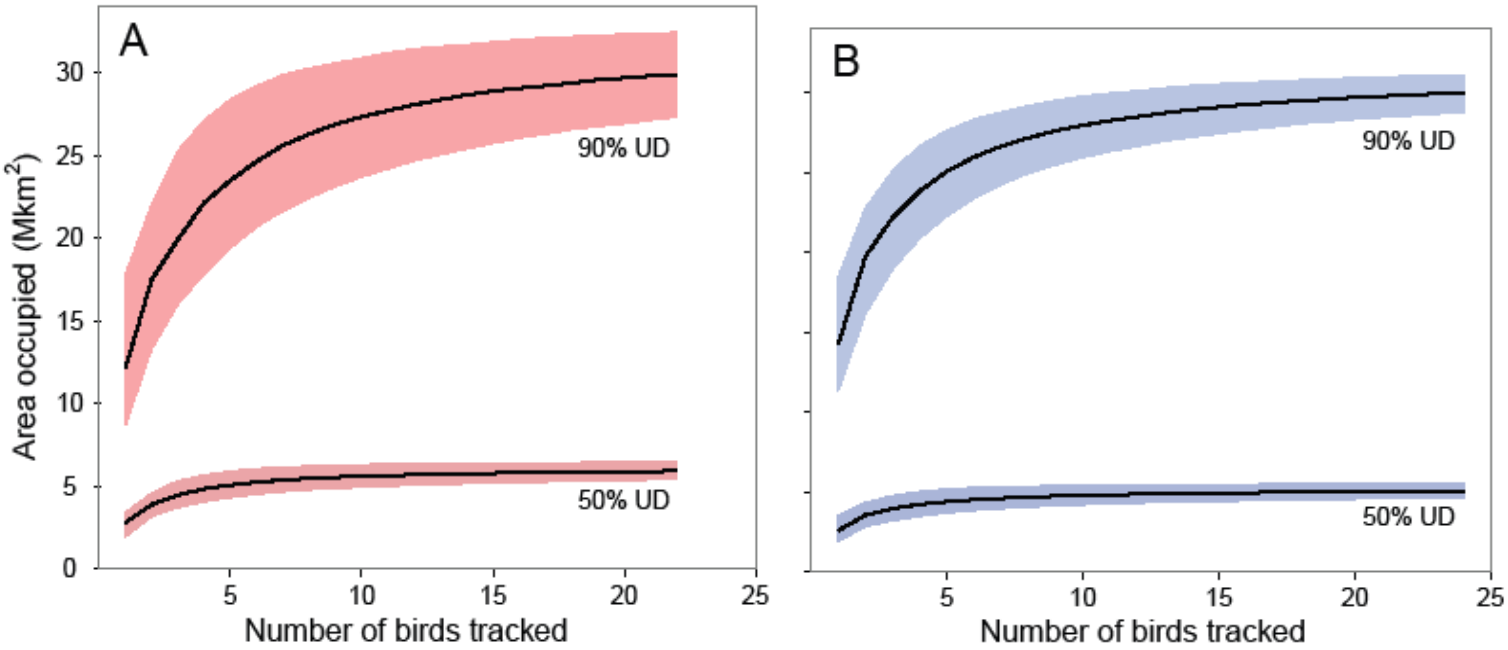


Figure A2.1. Bootstrapped area of 50% and 90% utilization distributions (UDs) of successful non-breeding grey-headed albatrosses relative to sample size for birds A) tracked from South Georgia (SG) and B) the Prince Edward Islands (PEI). The 25% and 75% quantiles (shaded areas; SG in red and PEI in blue) and means (black lines) of 1,000 bootstrap iterations are shown. Mkm^2 represents km^2 in millions.

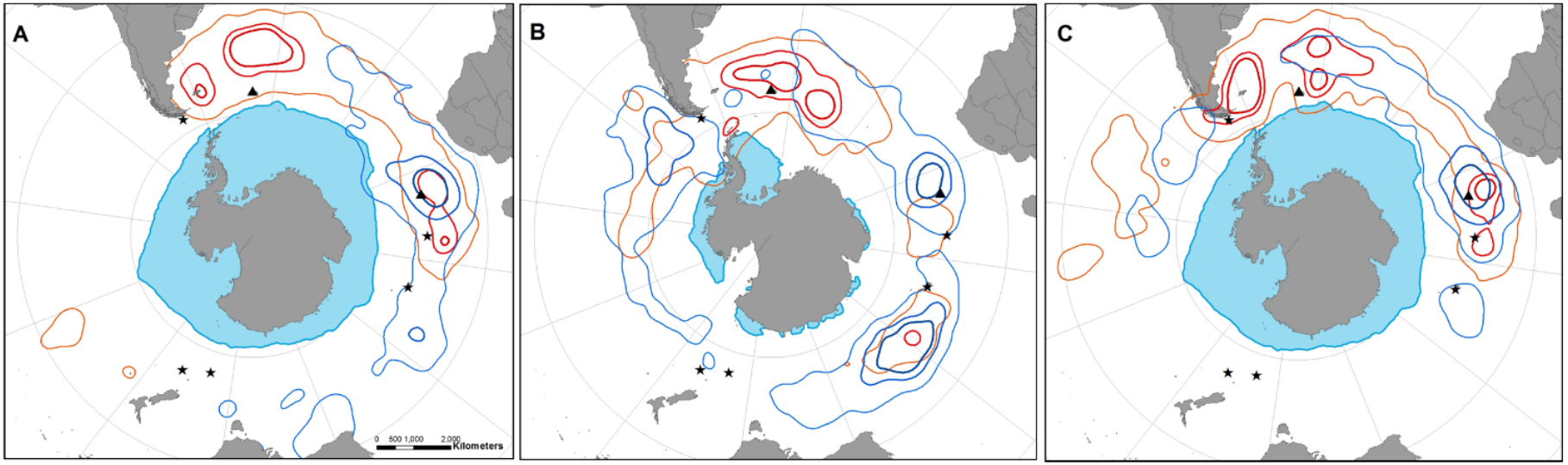


Figure A2.2. Population-level spatial segregation in non-breeding grey-headed albatross distributions is more pronounced during the non-breeding summer than non-breeding winter. Maps show 25%, 50% and 90% utilization distributions of non-breeding albatrosses from South Georgia (dark blue, blue and light blue) and Prince Edward Islands (dark red, red and orange) in the A) first non-breeding winter (colony departure to mid-September), B) non-breeding summer (mid-September to mid-May) and C) second non-breeding winter (mid-May to colony arrival). Black triangles represent the study colonies and black stars are other breeding colonies. The minimum summer and maximum winter sea ice extents (>15%) are also shown as blue polygons.

Table A2.2. Observed and randomized overlap (home-range method, PHR) of core (50%) and general (90%) UDs between different groups of grey-headed albatrosses; population (South Georgia or SG and Prince Edward Islands or PEI) by season, sex by population and season, and breeding outcome by season.

Class	50%			90%		
	Observed	Randomized	*P*	Observed	Randomized	*P*
Population						
Summer	0.03	0.64 + 0.07	**<0.001**	0.52	0.82 + 0.32	**<0.001**
Winter	0.25	0.71 + 0.09	**<0.001**	0.47	0.78 + 0.03	**<0.001**
Sex (All						
PEI	0.58	0.60 + 0.09	0.36	0.74	0.74 + 0.04	0.42
PEI	0.72	0.81 + 0.08	0.065	0.69	0.71 + 0.05	0.26
SG	0.41	0.68 + 0.09	**0.007**	0.70	0.67 + 0.05	0.81
SG	0.58	0.56 + 0.12	0.52	0.75	0.69 + 0.06	0.88
Breeding						
SG	0.55	0.72 + 0.06	**0.003**	0.67	0.77 + 0.04	**0.002**
SG	0.58	0.62 + 0.10	0.32	0.71	0.71 + 0.04	0.42

Breeding outcome comparisons are for SG only. Randomized overlaps are shown as a mean ± SD and P represents the proportion of randomized overlaps that were smaller than the observed. For more information see text in Appendix 2. Significant differences are shown in bold.

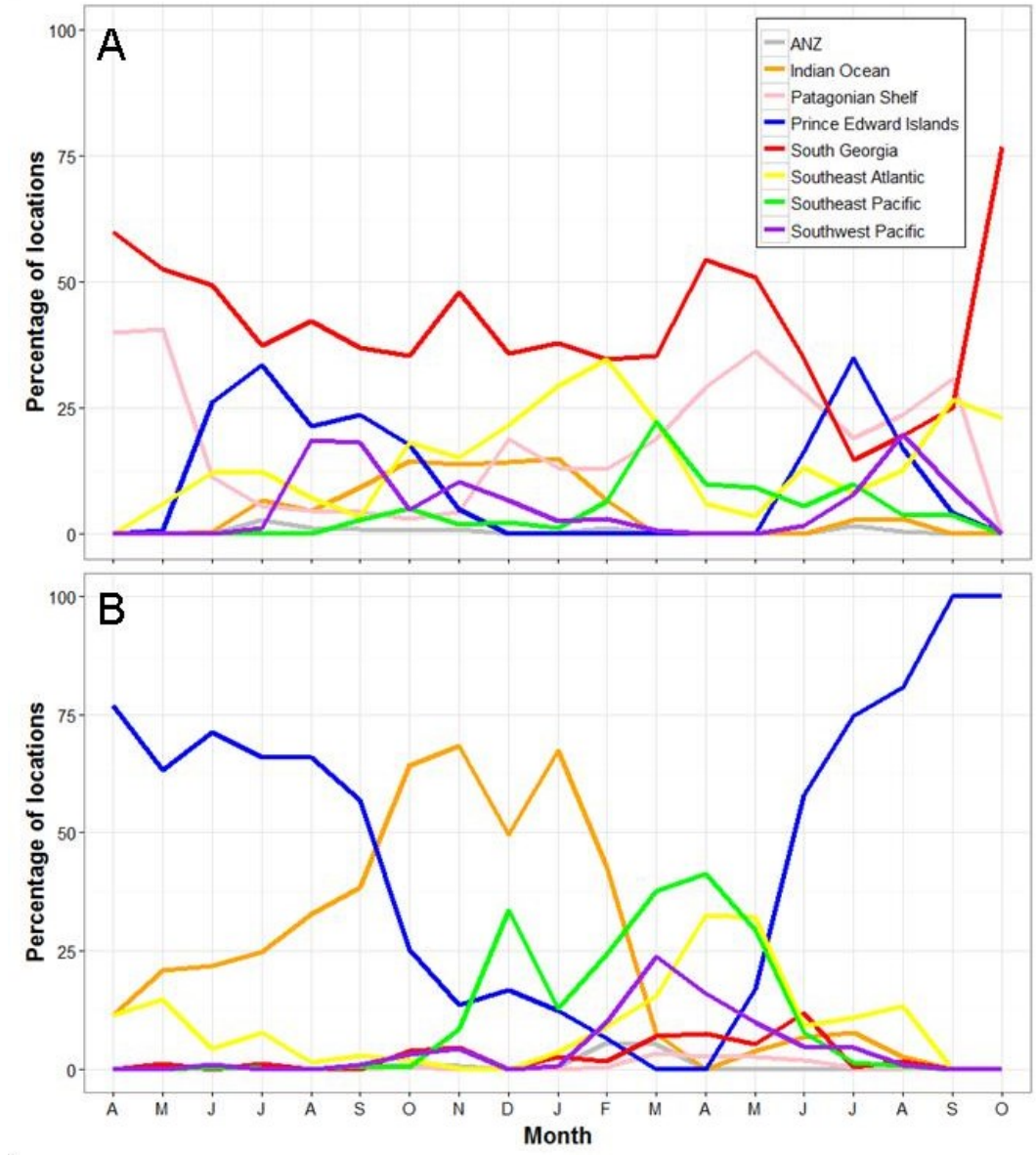


Figure A2.3. Proportion of successful migratory grey-headed albatrosses from A) South Georgia (SG) and B) Prince Edward Islands (PEI) in different oceanic sectors of the Southern Ocean over the duration of the non-breeding period by month. Notably, birds from both populations largely use different ocean sectors at different times. A large proportion of SG birds (around 40% of locations) remain in the SG area year-round, whereas the PEI birds do not appear to be resident during the summer, when they use the Indian Ocean and Southeast Pacific to a large degree. There is greatest overlap from June to August when the majority of PEI birds and a quarter of SG birds use the PEI region. Months are shown in initials along the x-axis, starting with April and ending in October the following year. "ANZ" indicates the region encompassing Australia and New Zealand.

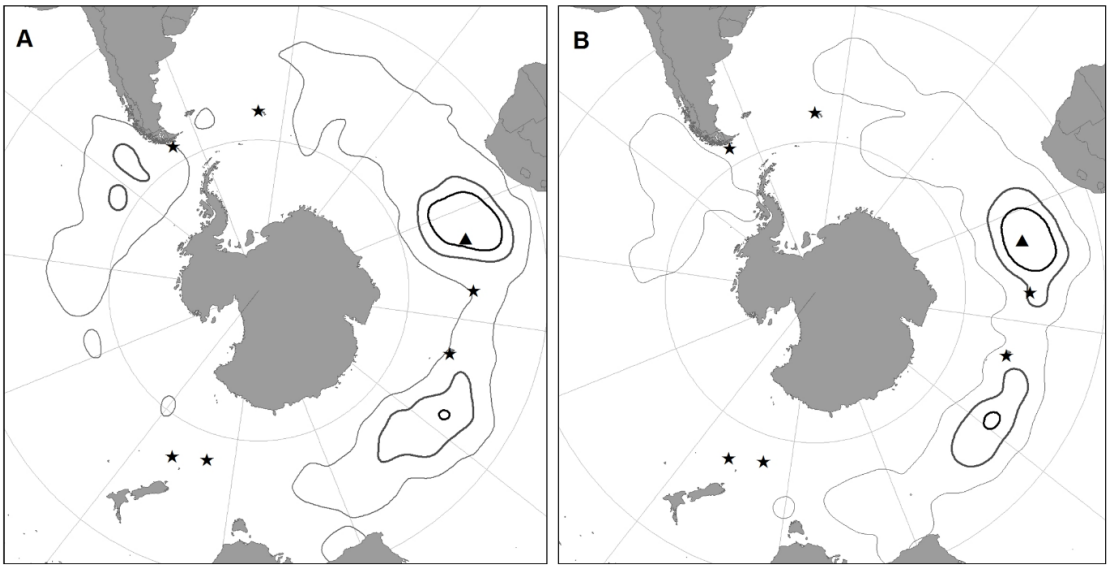


Figure A2.4. Non-breeding distributions of grey-headed albatrosses from the Prince Edward Islands tracked in A) 2002, and B) 2003. The 25%, 50% and 90% utilization distributions are shown.

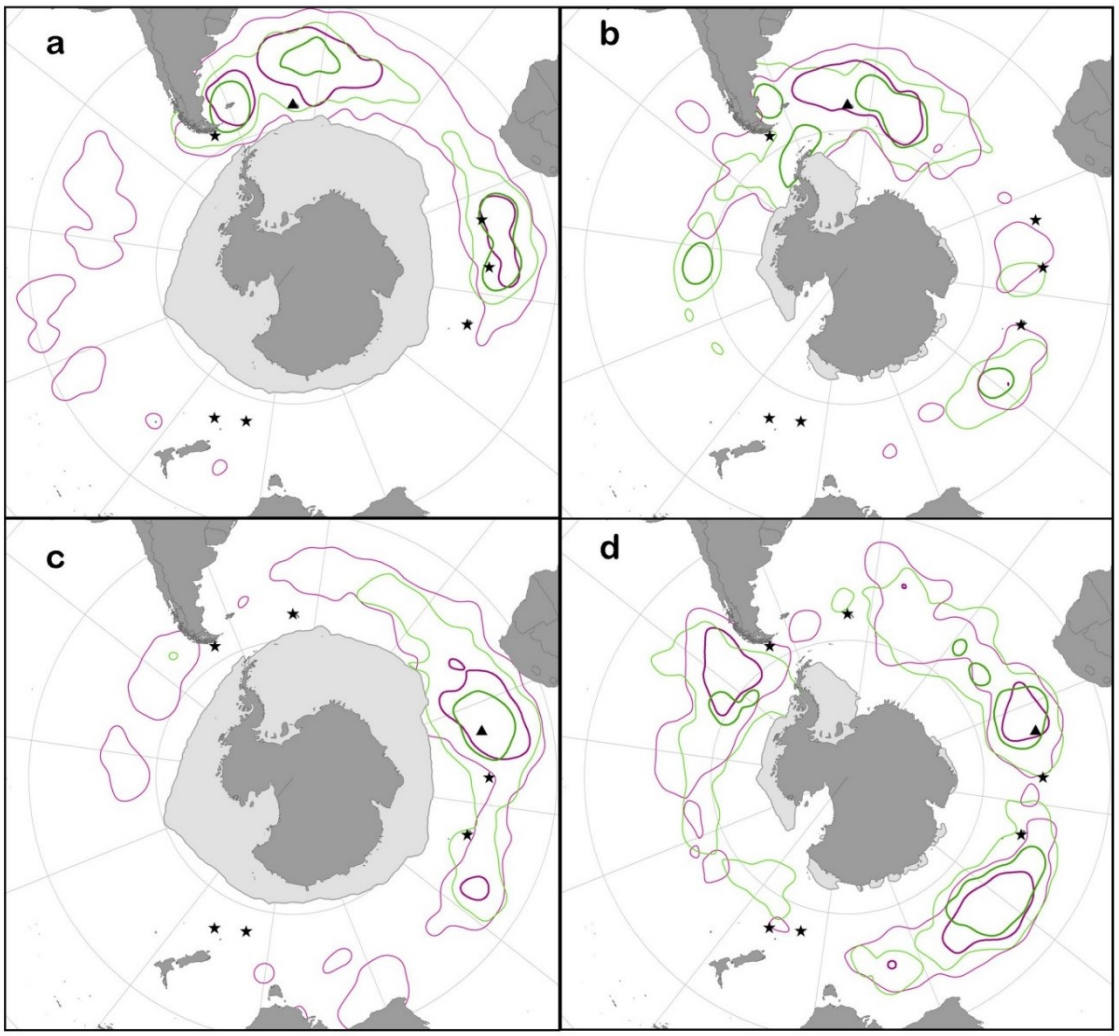


Figure A2.5. Sex differences in the non-breeding distributions of previously successful grey-headed albatrosses from South Georgia in a) winter and b) summer and Prince Edward Islands in c) winter and d) summer. The 50% and 90% utilization distributions are shown for males in purple and pink, respectively, and for females in dark and light green, respectively. Black triangles represent the study colonies and black stars are other breeding colonies. The minimum summer and maximum winter sea ice extents (>15%) are also shown as light grey polygons.

Table A2.3. List of variables used in habitat analysis. Where there is no description, averages were taken of all values within a 200 km buffer.

Variable	Abbrev.	Source	Temporal resolution	Spatial resolution	Description
Bathymetry	Depth	GEBCO	-	0.008°	-
Bathymetry gradient	Depth std	GEBCO	-	0.008°	Standard deviation of values in 200 km buffer
Sea surface temperature	SST	Pathfinder AVHRR v.5	Monthly	0.04°	-
Sea surface temperature gradient	SST std	Pathfinder AVHRR v.5	Monthly	0.04°	Standard deviation of values in 200 km buffer
Chlorophyll a concentration	Chl	SeaWiFS from Oceancolor	Monthly	0.08°	-
Eddy kinetic energy	EKE	AVISO absolute geostrophic current velocities	8-day	0.25°	-
Sea level anomaly	SLA	AVISO delayed-time updated MSLA	8-day	0.25°	-
Wind speed	Wind	ERS-2 and QuikSCAT from Ifremer	8-day	0.25°	-
Distance from own colony	Dist. own	Cost distance tool in ArcGis 10.1	-	-	Custom-generated raster of distance to own colony
Distance from nearest other colony	Dist. closest	Cost distance tool in ArcGis 10.1	-	-	Custom-generated raster of distance to other colonies

Table A2.4. Summary of the cross-validation of weekly spatial predictions, showing model performance (AUC) for each predictor type model. Models were constructed to represent the different extrinsic processes (predictor types) that best predict distribution patterns for each GHA population and season.

Model	Full model	Habitat model	Constraint model	Best model	ΔAIC
PEI Summer	**0.772** ± 0.137	0.741 ± 0.135	0.719 ± 0.122	Week +	80.18
	(0.500 – 0.951)	(0.501 – 1.000)	(0.500 – 0.907)	Model type	
PEI Winter	**0.806** ± 0.124	0.752 ± 0.109	0.772 ± 0.143	Week +	45.10
	(0.511 – 0.988)	(0.505 – 0.934)	(0.513 – 0.982)	Model type	
SG Summer	**0.753** ± 0.123	0.725 ± 0.101	0.703 ± 0.121	Week +	34.16
	(0.501 – 1.000)	(0.514 – 1.000)	(0.510 – 1.000)	Model type	
SG Winter	**0.772** ± 0.079	0.721 ± 0.059	0.702 ± 0.074	Week +	33.51
	(0.533 – 0.938)	(0.560 – 0.854)	(0.506 – 0.812)	Model type	

The habitat model contains just environmental predictors, the constraint model contains just distance predictors, and the full model contains all variables. I ran linear models to determine the effect of week and model type on AUCs, and the best model was judged by multi-model inference. For each population and season, AUCs were significantly influenced by predictor type and week, and in each case the best model is shown in bold. For each model means ± SD are for weekly AUC scores with ranges in parentheses.

Table A2.5. Summary of the performance of cross-validation of models with and without breeding outcome differences for South Georgia birds only.

Model	Interaction	No interaction	Difference	T test	P
Summer	**0.753** ± 0.110	0.726 ± 0.130	0.027 ± 0.075	t40 = 2.30	0.027
	(0.533 – 0.964)	(0.512 – 0.917)	(-0.121 – 0.269)		
Winter	0.753 ± 0.130	0.758 ± 0.135	-0.005 ± 0.052	t40 =-0.59	0.555
	(0.519 - 0.969)	(0.508 – 0.961)	(-0.159 – 0.107)		

I measured model performance using AUC scores at the individual level. Interaction indicates that models included breeding outcome-specific smoothers for each environmental variable and the differences between the AUC scores with and without the interaction for each individual are also shown. Where there are significant differences between AUC scores with and without the interaction, they are emphasized in bold along with the best model. For each model means ± SD are shown with ranges in parentheses.

Table A2.6. Summary of the performance of the cross-validation of models with and without sex-differences for successful birds from both populations in summer and winter.

Model	Interaction	No interaction	Difference	T test	P
PEI Summer	0.780 ± 0.093	0.787 ± 0.081	-0.007 ± 0.048	t22 = -0.66	0.518
	(0.510 – 0.892)	(0.639 – 0.901)	(-0.191 – 0.048)		
PEI Winter	0.804 ± 0.073	0.791 ± 0.080	0.014 ± 0.046	t23 = 1.46	0.157
	(0.660 – 0.925)	(0.660 – 0.916)	(-0.084 – 0.125)		
SG Summer	0.763 ± 0.099	0.745 ± 0.009	0.009 ± 0.052	t20 = -0.79	0.437
	(0.557 – 0.954)	(0.554 – 0.929)	(-0.050 – 0.185)		
SG Winter	0.758 ± 0.076	0.761 ± 0.074	-0.003 ± 0.021	t20 = -0.61	0.549
	(0.639 – 0.912)	(0.648 – 0.904)	(-0.048 – 0.039)		

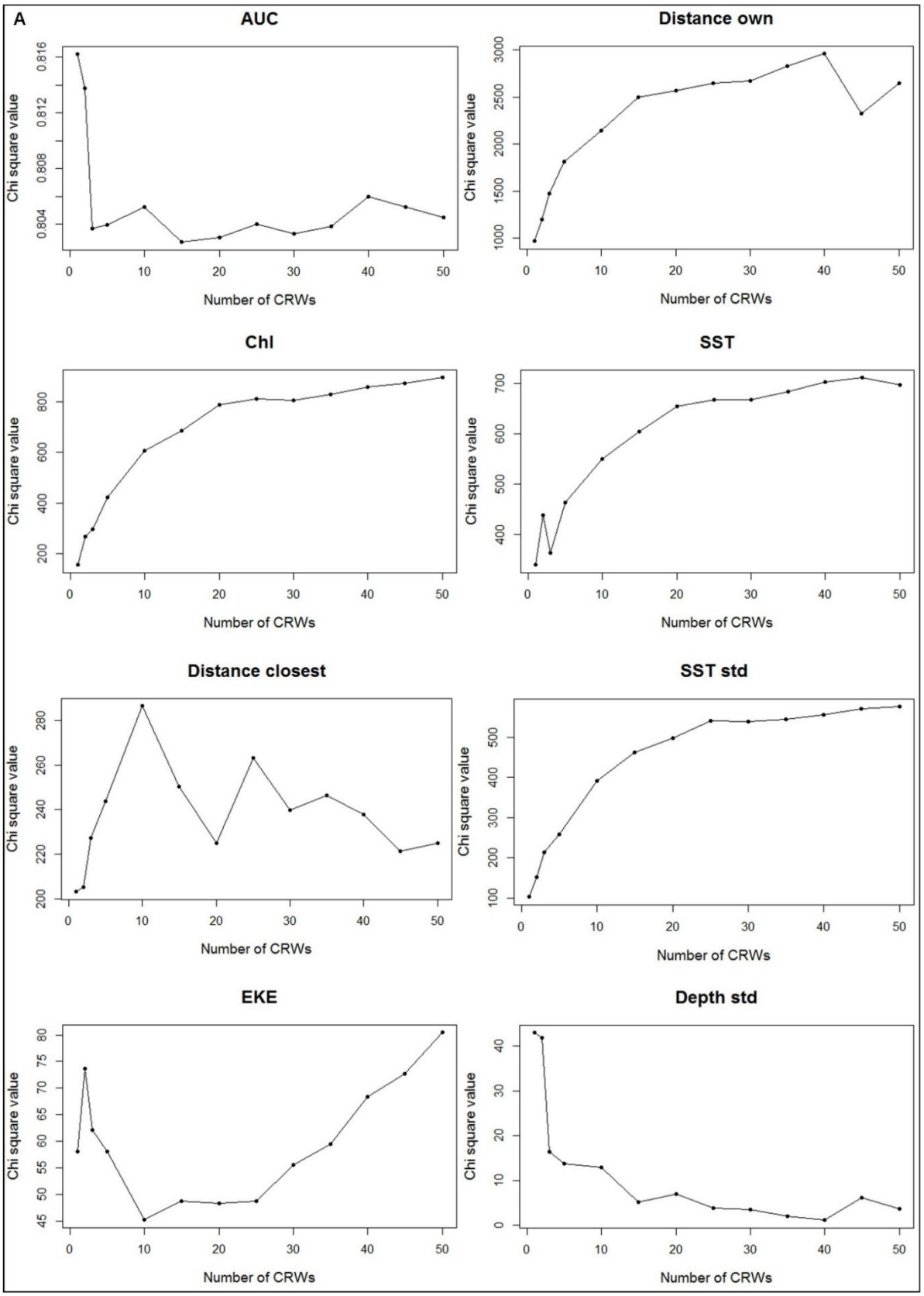
I measured model performance using AUC scores at the individual level. Interaction indicates that models include sex-specific smoothers for each environmental variable and the differences between the AUC scores with and without the interaction for each individual are also shown. In each case, there were no significant differences between AUC scores with and without the interaction. For each model, means ± SD are shown with ranges in parentheses.

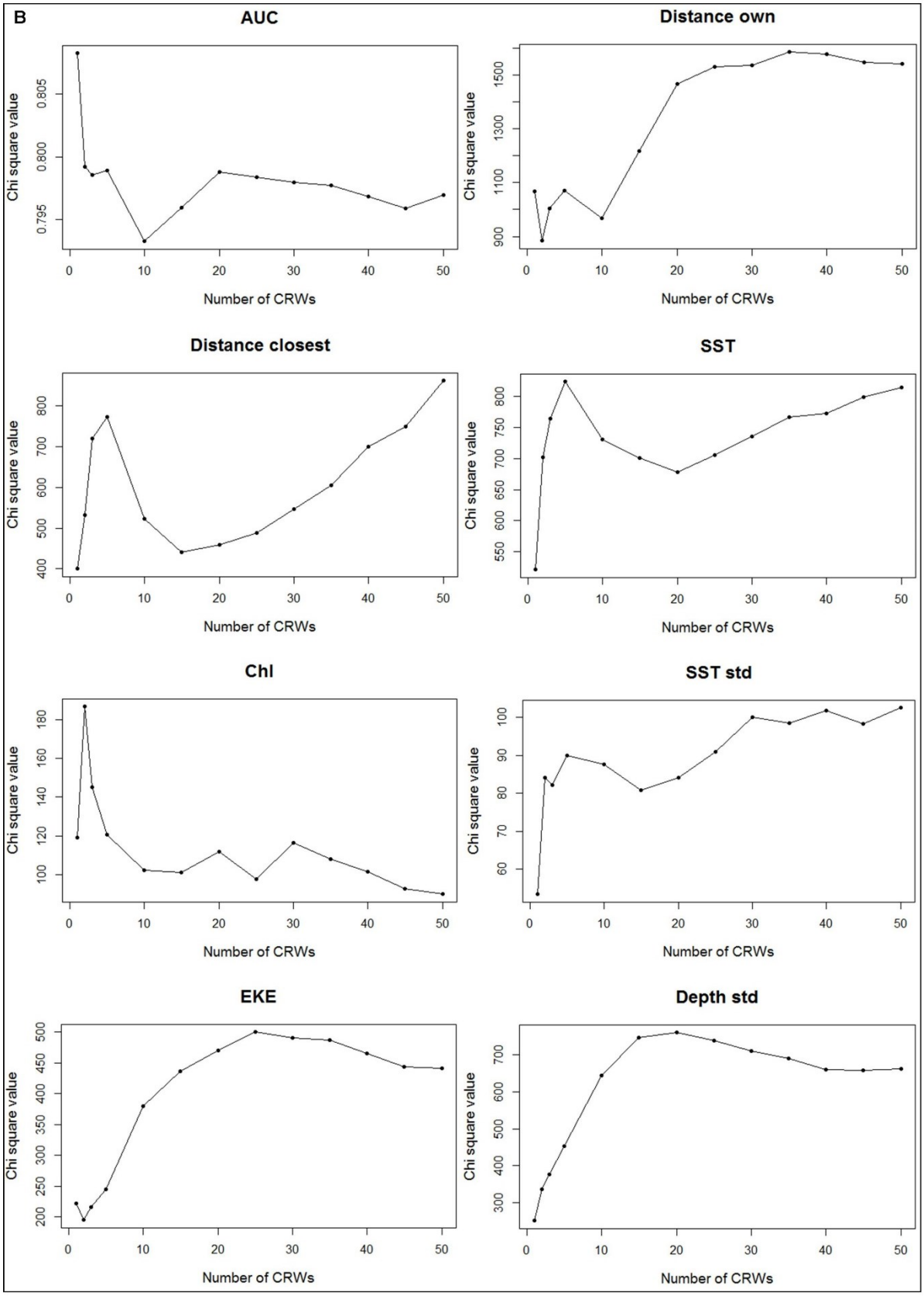
Table A2.7. Model selection summaries for birds tracked from PEI and SG during summer and winter.

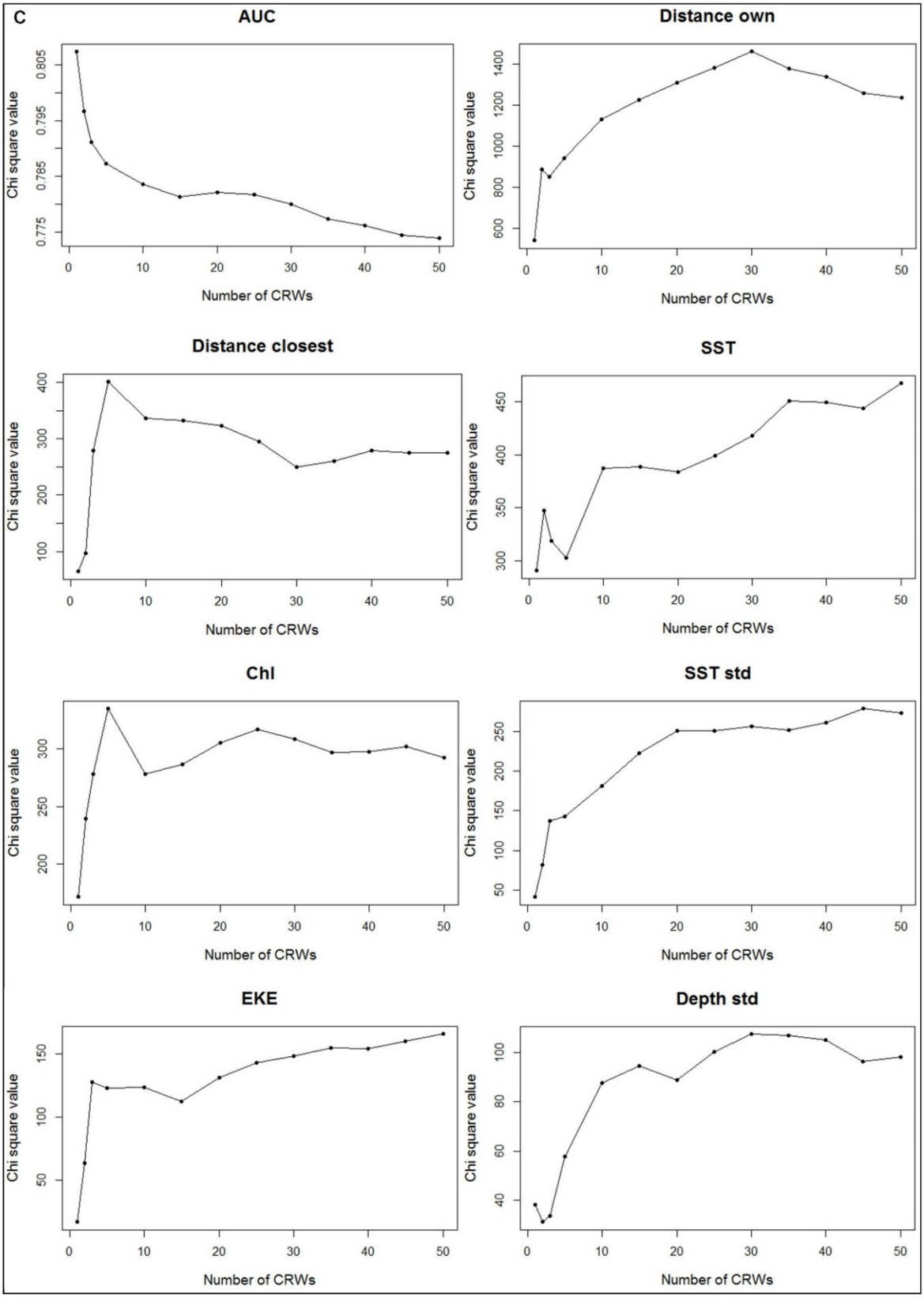
Model	LogLik	AICc	ΔAICc	Weight
PEI summer				
All variables	-34380.0	68833.67	0.00	1.00
All variables except SLA	-34400.0	68869.02	35.35	< 0.01
All variables except Depth	-34431.5	68924.60	90.94	< 0.01
All variables except SST std	-34436.7	68934.43	100.76	< 0.01
PEI winter				
All variables	-30736.7	61540.93	0.00	0.77
All variables except Depth std	-30738.5	61543.31	2.37	0.23
All variables except SLA	-30768.1	61592.22	51.29	<0.01
All variables except EKE	-30766.8	61593.65	52.71	<0.01
All variables except Depth std and SLA	-30770.2	61594.80	53.86	<0.01
SG summer				
All variables	-29951.5	59965.50	0.00	0.96
All variables except SLA	-29955.4	59972.07	6.57	0.03

All variables except Wind speed	-29966.2	59983.49	17.99	<0.01
All variables except SLA and Wind speed	-29971.0	59991.16	25.66	<0.01
All variables except Depth std	-29968.2	59991.58	26.01	<0.01
SG winter				
All variables	-25573.0	51208.81	0.00	1.00
All variables except SLA	-25622.0	51302.88	94.07	< 0.01
All variables except Depth std	-25627.6	51309.89	101.08	< 0.01
All variables except Wind speed	-25641.9	51340.98	132.17	< 0.01
All variables except EKE	-25657.7	51372.55	163.74	< 0.01

For each model, all combinations were run and ranked based on their parsimony. The five best models are shown.


A
AUC
Chi square value
Number of CRWs
Distance own
Chi square value
Number of CRWs
Chl
Chi square value
Number of CRWs
SST
Chi square value
Number of CRWs
Distance closest
Chi square value
Number of CRWs
SST std
Chi square value
Number of CRWs
EKE
Chi square value
Number of CRWs
Depth std
Chi square value
Number of CRWs


B
AUC
Chi square value
Number of CRWs
Distance own
Distance closest
SST
Chl
SST std
EKE
Depth std


C
AUC
Chi square value
Number of CRWs
Distance own
Chi square value
Number of CRWs
Distance closest
Chi square value
Number of CRWs
SST
Chi square value
Number of CRWs
Chl
Chi square value
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SST std
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EKE
Chi square value
Number of CRWs
Depth std
Chi square value
Number of CRWs

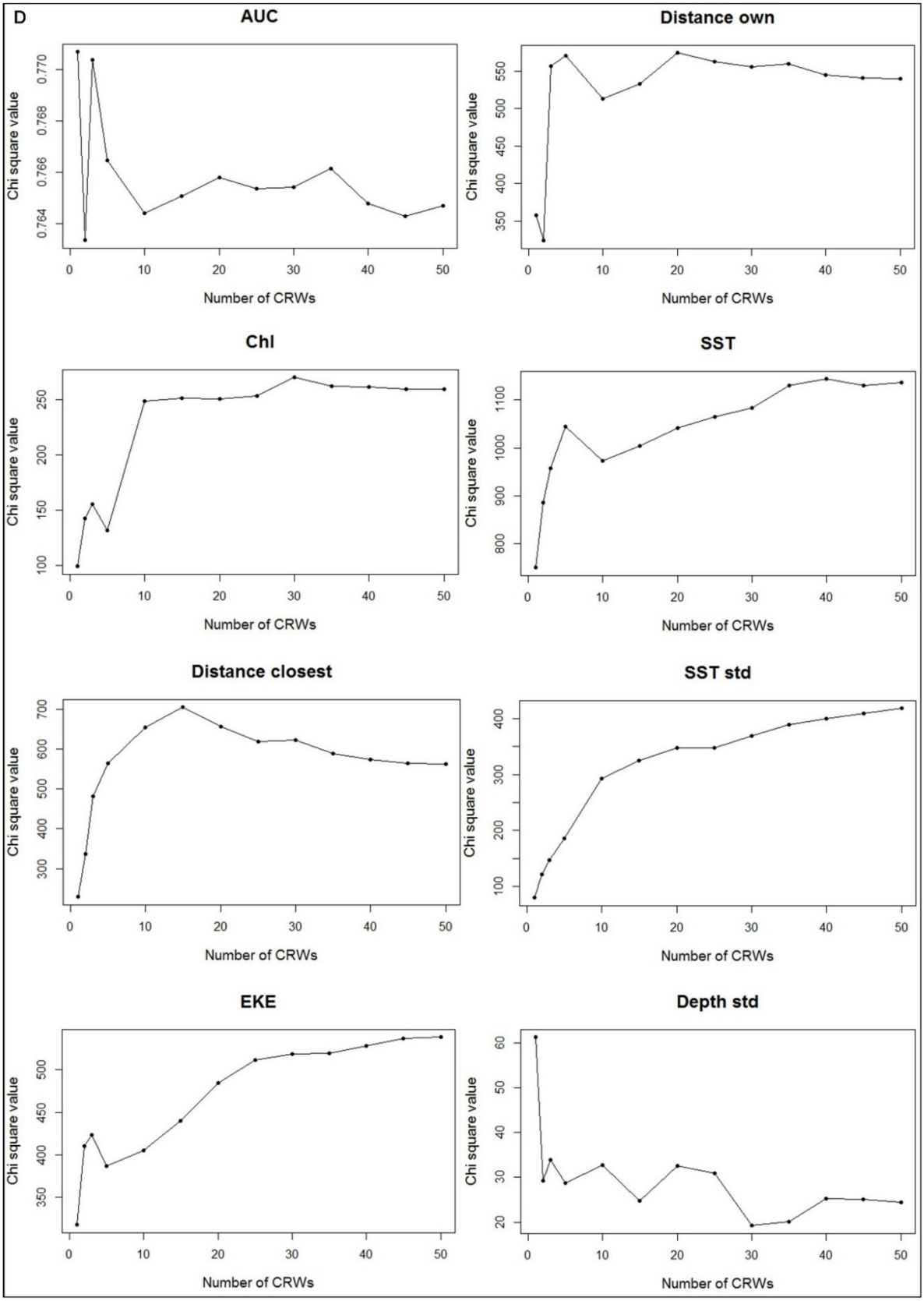
D
AUC
Distance own
Chl
SST
Distance closest
SST std
EKE
Depth std
Chi square value
Number of CRWs

Figure A2.6. Chi-square values of key predictor variables (explaining >1% deviance explained) and model performance scores (AUC) with increasing number of correlated random walks (CRWs) for A) PEI winter B) PEI summer C) SG winter and D) SG summer models.

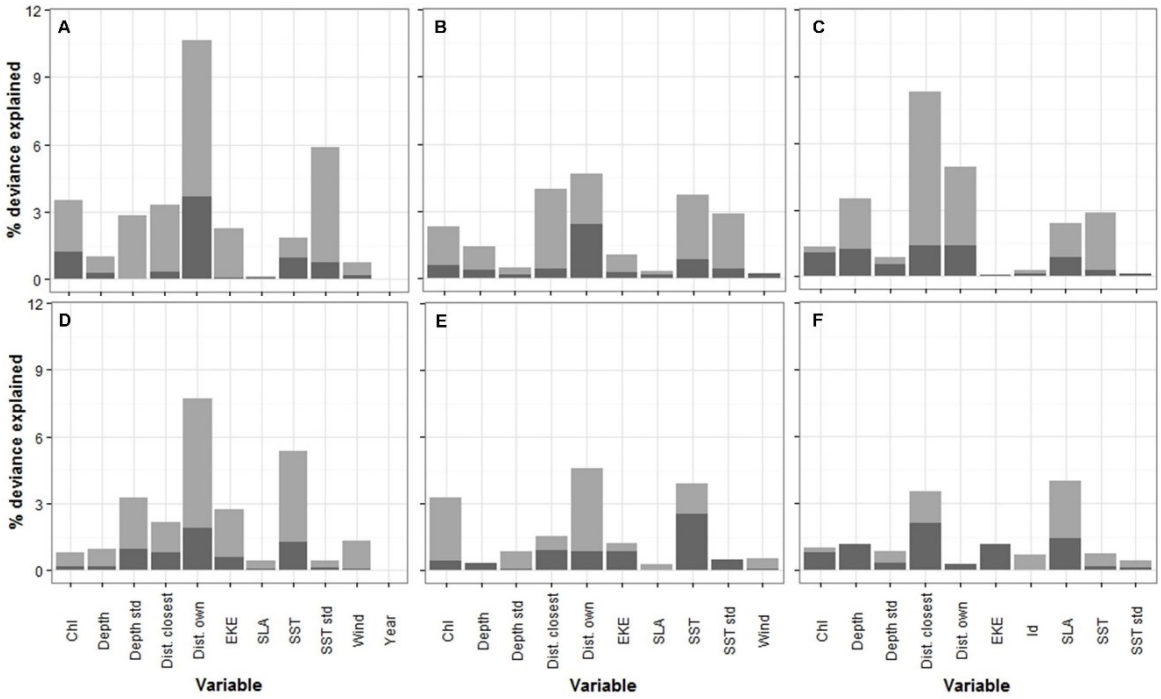

Figure A2.7. The percentage of deviance explained by important variables (those with >1% deviance explained) for previously successful grey-headed albatrosses for the following models; A) PEI winter, B) SG winter, D) PEI summer and E) SG summer. Also shown are variables for SG failed birds during C) winter and F) summer. Deviance is split into unique deviance explained just by that variable (black), and deviance shared with other variables (grey).

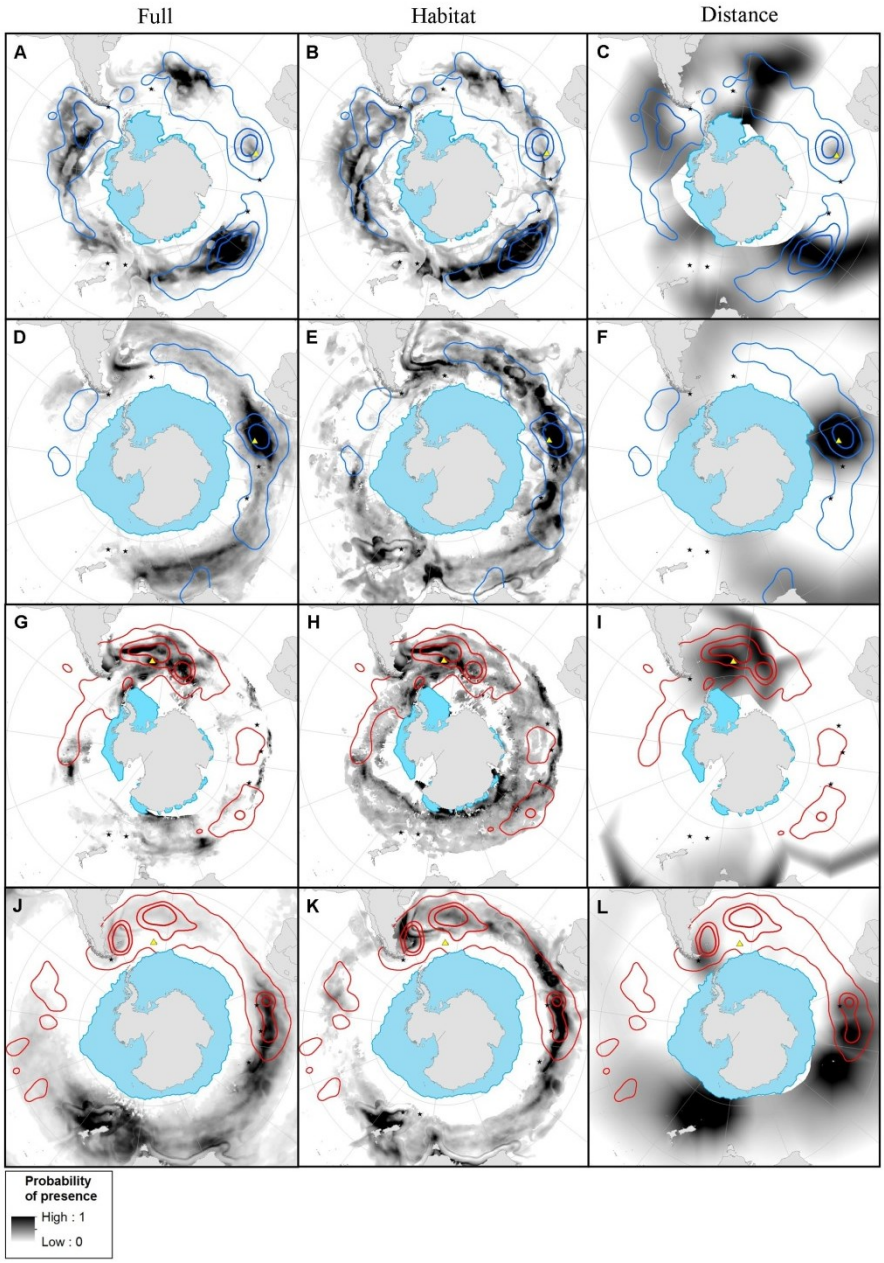

Figure A2.8. Map of the spatial predictions from the full models (A, D, G, J), those just taking into account habitat preferences (B, E, H, K), and those taking into account accessibility and competition (C, F, I, L). Maps are of suitable habitat from model predictions, scaled to 1 to show probability of presence of birds from different populations in summer and winter; PEI winter (A - C), SG winter (D – F), PEI summer (G – I) and SG summer (J – L). 25%, 50% and 90% kernels of observed distributions are shown for PEI and SG birds in blue or red, respectively. The minimum summer or maximum winter sea ice extents (>15%) are also shown as blue polygons and the colonies of origin as yellow triangles

9. Appendices

APPENDIX 3 – SUPPLEMENTARY MATERIAL FOR CHAPTER 4

Table A3.1. Summary of GLMM for the effects of sex, year, and the interaction between sex and year on the timing and characteristics of movements and distribution of Murphy's petrels.

	Sex	Year	Sex:Year	*d.f.*	AICc	ΔAIC	AICw
Last night at colony	-	-	-	3	300.4	1.10	0.44
Migration							
Outbound departure date	-	-	-	3	346.7	0.00	0.43
Outbound arrival date	-	-	-	3	326.2	0.00	0.48
Outbound duration	-	-	-	3	169.3	0.00	0.37
Inbound departure date	-	-	-	3	237.0	0.00	0.63
Inbound arrival date	-	-	-	3	262.4	0.00	0.62
Inbound duration	-	-	-	3	163.4	0.00	0.60
Non-breeding							
NB duration	-	-	-	3	235.7	0.67	0.30
Mean longitude	-	-	-	3	248.5	0.00	0.49
Mean latitude	-	X	-	4	146.9	0.00	0.64
Pre-laying exodus							
First night back at	-	-	-	3	273.0	0.00	0.58
Departure date	-	X	-	4	211.1	0.00	0.51
Return date	-	X	-	4	207.3	0.00	0.64
Duration	-	X	-	5	160.2	1.30	0.28
Max. distance colony	X	-	-	4	479.5	1.14	0.31
Cumulative distance	-	-	-	3	632.7	0.00	0.50
Mean longitude	-	-	-	3	245.9	1.90	0.12
Mean latitude	-	-	-	3	158.1	0.07	0.26
Incubation							
Departure date 1st trip	X	-	-	4	191.2	0.00	0.77
Return date 1st trip	X	-	-	4	197.4	0.00	0.63
Duration 1st trip*	-	X	-	4	154.6	0.00	0.51
Max. dist. colony 1st trip*	-	-	-	4	443.3	0.00¥	0.58
Cumulative dist. 1st trip*	-	-	-	4	528.0	0.00¥	0.53
Proportion long trips	-	-	-	2	37.1	0.00	0.60
Mean longitude	-	-	-	3	206.4	0.00	0.51
Mean latitude	-	-	-	3	177.8	0.43	0.24

X indicates predictors that were retained by the most parsimonious models, and - indicates predictors that were not retained in the analysis. * indicates that incubation trip type was also included as a predictor and ¥ that it was retained as an important predictor. Where ΔAIC > 0,*

another model had a lower AIC, but not to the extent of incurring the penalty of extra parameters.

Table A3.2. Summary of GLMM for the effects of breeding stage, daylight or darkness (LoD), year, and the interaction between LoD and breeding stage, on the activity patterns of Murphy's petrels.

LoD	Stage	Year	LoD:Stage	d.f.	AICc	ΔAICc	AICw
Proportion of time on water							
X	X	X	X	13	6264.3	0.00	0.69
X	X	-	X	12	6265.9	1.58	0.31
X	X	X	-	9	6777.2	512.86	0.00
X	X	-	-	8	6778.6	514.23	0.00
-	X	X	-	8	7330.3	1065.92	0.00
Number of landings							
X	X	-	X	12	-4626.9	0.00	0.50
X	X	X	X	13	-4626.8	0.01	0.50
X	X	-	-	8	-4298.2	328.70	0.00
X	X	X	-	9	-4298.1	328.71	0.00
-	X	-	-	7	-1969.5	2657.38	0.00
Flight bout duration							
X	X	X	X	13	11069.5	0.00	0.83
X	X	-	X	12	11072.6	3.10	0.18
X	X	X	-	9	11413.6	344.14	0.00
X	X	-	-	8	11416.5	347.04	0.00
-	X	X	-	8	11419.6	350.17	0.00
Number of flight bouts							
X	X	X	X	13	-4749.3	0.00	0.53
X	X	-	X	12	-4749.1	0.25	0.47
X	X	X	-	9	-4526.7	222.62	0.00
X	X	-	-	8	-4526.4	222.87	0.00
-	X	X	-	7	-2757.6	19991.71	0.00

X indicates predictors that were retained, whilst - indicates predictors that were not retained in the analysis.

Figure A3.1. Modelled parameter estimates from GLMM explaining a) the proportion of time spent on water, b) the number of landings, c) flight bout durations and d) the number of flight bouts for each breeding stage in daylight and darkness ± standard errors. Outward and Return indicate both migration periods.

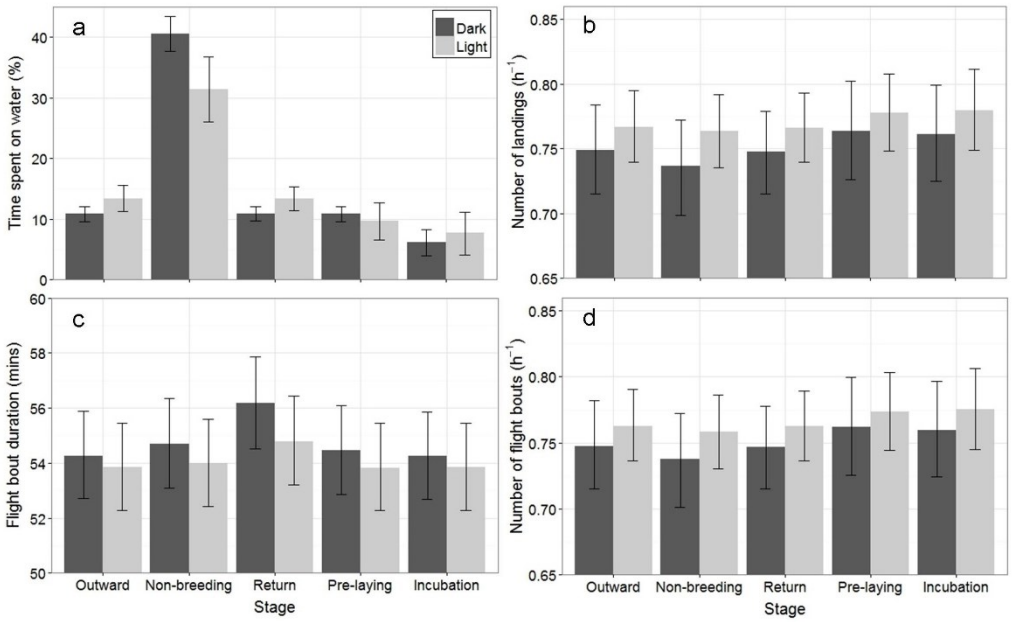

Table A3.3. Summary of the top five GLMMs for the effects of sex, year, isopleth level (0-50% or 51-95%) and the interaction between isopleth and sex on the habitat characteristics of Murphy's petrels for each breeding stage.

Isopleth	Sex	Year	Isopleth:Sex	d.f.	AICc	ΔAICc	AICw
Chlorophyll							
Non-breeding							
-	-	-	-	3	-357.5	0.00	0.30
X	-	-	-	4	-356.2	1.28	0.16
-	X	-	-	4	-355.8	1.72	0.13
-	-	X	-	4	-355.6	1.85	0.12
X	X	-	X	6	-354.6	2.86	0.07
Pre-laying exodus							
X	X	-	-	5	-277.2	0.00	0.31
X	X	-	X	6	-277.2	0.02	0.30
X	X	X	-	6	-275.5	1.74	0.13
X	X	X	X	7	-275.4	1.80	0.12
X	-	-	-	4	-274.9	2.28	0.10
Incubation							
X	-	-	-	4	-281.8	0.00	0.24
-	-	-	-	3	-281.8	0.06*	0.23
X	-	X	-	5	-280.6	1.22	0.13

	-	X	-	4	-280.5	1.35	0.12
-	X	-	-	4	-279.7	2.11	0.08
Late-breeding							
X	X	X	X	7	-356.7	0.00	0.54
X	-	X	-	5	-354.4	2.28	0.17
X	X	X	-	6	-353.6	3.08	0.12
X	X	-	X	6	-353.5	3.22	0.11
X	-	-	-	4	-351.5	5.22	0.04
Sea surface temperature							
Non-breeding							
X	-	X	-	5	262.8	0.00	0.57
X	X	X	-	6	265.1	2.29	0.18
X	X	X	X	7	265.7	2.88	0.14
X	-	-	-	4	267.7	4.94	0.05
-	-	X	-	4	269.0	6.18	0.03
Pre-laying exodus							
X	-	X	-	5	278.0	0.00	0.31
X	X	-	-	6	278.6	0.55	0.24
X	-	-	-	4	278.9	1.90*	0.20
X	X	-	-	5	279.6	1.55	0.14
X	X	X	X	7	278.1	3.08	0.07
Incubation							
-	-	X	-	4	281.8	0.00	0.20
-	-	-	-	3	281.9	0.07*	0.19
-	X	-	-	4	281.9	0.13	0.19
-	X	X	-	5	282.1	0.31	0.17
X	-	-	-	4	284.2	2.37	0.06
Late-breeding							
-	-	-	-	3	310.4	0.00	0.31
X	-	-	-	4	311.4	0.96	0.19
-	-	X	-	4	311.9	1.49	0.15
-	X	-	-	4	312.6	2.15	0.11
X	-	X	-	5	312.9	2.50	0.09
Depth							
Non-breeding							
-	-	-	-	3	1022.5	0.00	0.35
X	-	-	-	4	1023.9	1.39	0.18
-	-	X	-	4	1024.5	1.97	0.13
-	X	-	-	4	1024.6	2.07	0.13
X	-	X	-	5	1026.0	3.42	0.06
Pre-laying exodus							
X	X	-	-	5	953.2	0.00	0.42

X	X	-	X	6	954.4	1.15	0.23
X	X	X	-	6	955.2	1.92	0.16
X	X	X	X	7	956.4	3.16	0.09
X	-	-	-	4	956.7	3.42	0.08
Incubation							
X	-	-	-	4	787.8	0.00	0.39
X	-	X	-	5	789.2	1.37	0.20
X	X	-	-	5	789.5	1.72	0.17
X	X	X	-	6	791.1	3.27	0.08
X	X	-	X	6	792.0	4.17	0.05
Late-breeding							
X	-	X	-	5	930.6	0.00	0.42
X	X	X	-	6	930.8	0.16	0.39
X	X	X	X	7	932.7	2.07	0.15
X	-	-	-	4	937.1	6.49	0.02
X	X	-	-	5	937.3	6.73	0.01

*All other interactions were not significant so are not included. X indicates predictors that were retained and - indicates predictors that were not retained. * indicates that another model had a lower AIC, but not to the extent of incurring the penalty of extra parameters.*

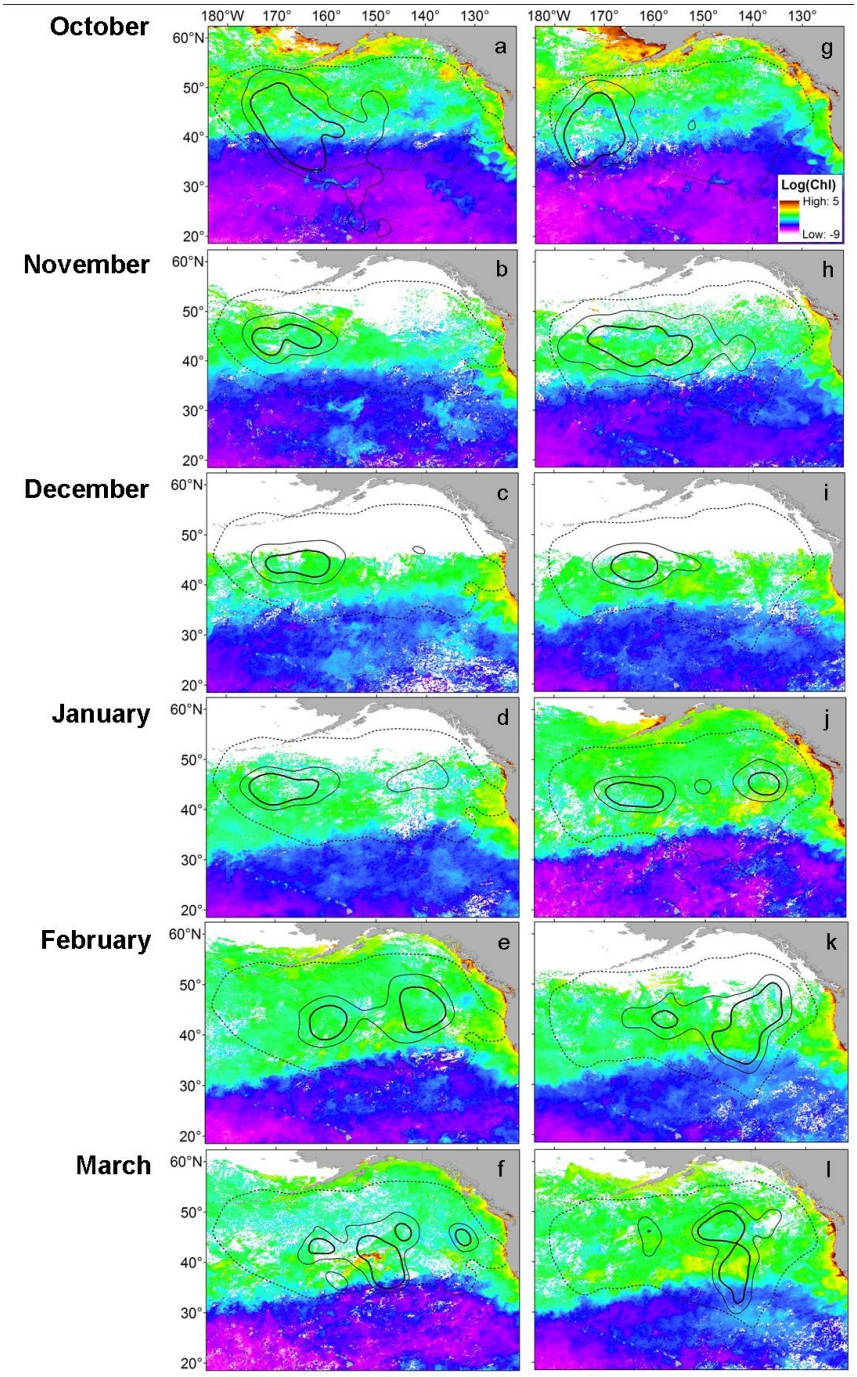

Figure A2.2. Monthly core (25% and 50% UDs, solid) and general use areas (95% UDs, dashed) of Murphy's petrels during a-f) 2011/12 and g-l) 2012/13 non-breeding seasons, overlaid with monthly log chlorophyll *a* concentration.

APPENDIX 4 – SUPPLEMENTARY MATERIAL FOR CHAPTER 5

Methods

Data processing

Data were filtered to remove unrealistic flights speeds of >40 kmh^{-1} sustained over a 48 h period (Phillips et al., 2004b). Loggers tested for saltwater immersion every 3 s with MK3–5 loggers storing the sum of positive tests at the end of each 10 min period. MK7 loggers recorded the time of every transition from wet to dry and vice versa that lasted >= 6 s. In order to standardise the resolution of outputs from devices, data from MK7 loggers were resampled to 10 min periods. A wet bout was defined as a 10 min period during which at least one wet event was recorded, and a flight bout as a continuous 10 min period spent entirely dry. Each period was categorised as daylight or darkness based on the timing of civil twilight from the light data. Loggers did not record the exact number of landings and take-offs in a given 10 min interval, and so are likely to underestimate the true number; however, studies using high resolution devices have found wandering albatrosses land a limited number of times in a 10 min period (Weimerskirch et al., 1997), and also a close correlation between the number wet bouts (every 10 min) and the number of landings (every 10 s), indicating that they are suitable proxies for foraging activity (Phalan et al., 2007).

Stable isotope analysis

Feathers were cleaned of surface lipids and contaminants using two successive 2:1 chloroform:methanol rinses for 30 minutes in an ultrasonic bath, followed by two successive 2:1 methanol:chloroform rinses and a final water rinse. Feathers were freeze-dried and homogenized by cutting into small pieces using stainless steel scissors and ~0.4 mg aliquots were weighed into tin capsules. Nitrogen and carbon isotope ratios were determined by a continuous-flow mass spectrometer (Thermo Scientific (Bremen, Germany) Delta V) coupled to an elemental analyser (Elementar (Langenselbold, Germany) vario PYRO cube). Analyses were conducted at the Natural Environment Research Council (NERC) Life Sciences Mass Spectrometry Facility in East Kilbride. In order to correct for instrument drift, three internal laboratory standards were analyzed for every 10 tissue samples. Isotope ratios are reported as δ-values and expressed as ‰

according to the equation $\delta X = [R_{sample}/R_{standard})-1]$, where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$ and $R_{standard}$ is the ratio of international references Vienna PeeDee Belemnite for carbon and atmospheric N^2 (AIC) for nitrogen. Replicate measurements of internal lab standards indicated measurement precision of ± 0.06 ‰ for $\delta^{13}C$ and ± 0.18 ‰ for $\delta^{15}N$.

Age-related variation in breeding success

Although both age and experience have been used in studies of ageing (Angelier et al., 2006; Froy et al., 2015), the total number of breeding attempts was highly correlated with age in the tracking sample (Spearman's rank correlation = 0.93, S = 7088, $P <$ 0.001). While I was able to calculate a minimum age for birds where the exact age was not known, it was not possible to estimate an accurate value of the minimum number of breeding attempts of these birds (as in Lecomte *et al.* 2010), and so age was chosen as a predictor. Analyses only included adults that had made at least one previous breeding attempt. A conservative approach was taken where exact age was unknown; all birds with a minimum age of <25 years were removed, as this was the cut-off for the oldest age class, when used as a categorical variable (below). The final sample included birds aged 9 – 33 years, a range covering the major changes in breeding parameters across the lifespan of wandering albatrosses from Bird Island (Froy et al., 2013). Additionally, to maintain independence, I randomly removed one year of data for individuals tracked in two of the study years. Analyses excluded tracking data from the single bird that failed in chick rearing, as the subsequent non-breeding period is markedly shorter than in birds which fail in incubation or fledge the chick.

Colony-wide breeding success

I investigated age-related variation in breeding success of the whole monitored population during the study years (2009 and 2010) to: a) determine if the pattern in the tracking sample reflected that of the wider population, and b) to determine annual variability in the pattern of reproductive senescence. I removed individuals whose age was uncertain and removed ages with fewer than 5 individuals. I modelled breeding success using GLM for each year and sex separately, with age as both a linear and quadratic variable (Froy et al., 2013; Lecomte et al., 2010), and carried out model selection as described in the main text. (Table A4.2).

Randomization procedure

In order to test whether albatrosses differed in their spatial distributions by age, sex and year of tracking, I used a randomization procedure previously described (Breed et al., 2006; Clay et al., 2016). Individuals were split into three age classes: young (6 – 14 years), middle-aged (15 – 24 years) and old-aged (25+ years) birds. I created utilization distribution (UD) kernels to represent core (50% UD) and general use areas (95% UD) for each individual using a grid size of 50km and smoothing factor of 200 km (Phillips et al., 2005, 2004a), and merged them to assign them equal weighting. I used Bhattacharyya's affinity (BA), a metric of similarity between two distributions ranging from 0 (no similarity) to 1 (identical UDs), as a measure of spatial overlap (Fieberg and Kochanny, 2005). I randomly reassigned bird identities and calculated overlap scores for 1,000 iterations, maintaining the same ratios observed. *P*-values were determined as the proportion of randomized overlaps that were smaller than the observed (Breed et al., 2006). This method was validated using another metric of spatial overlap, the utilization distribution overlap index (UDOI, Fieberg & Kochanny 2005), with the two producing similar results (Table S3). Kernel analysis and spatial overlaps were run in the R package *adehabitatHR* (Calenge, 2006).

Distance variables

In order to calculate distances from the colony, a cost raster surface was created in the South Pole Lambert Azimuthal Equal Area projection in ArcGIS 10.1 using the *cost distance* function, with paths not allowed to cross land barriers. A value of the distance from the colony value was extracted for each location and the median for each individual was included in analysis. Distances travelled per day were calculated using the *adehabitatLT* package in R (Calenge, 2006), considering only consecutive locations fewer than 24 hours apart to account for loss of locations due to shading of light curves at dawn or dusk or due to missing locations around the equinox period. The total distance travelled was divided by the number of days and the median value was extracted for each individual. Although locations have large error (Phillips et al., 2004b), these calculations are likely to underestimate real distances travelled due to lack of tortuoisty of geolocator tracks compared with tracks derived from GPS locations (Edwards et al., 2016). As the error is likely to be similar across individuals, this should not influence among-individual comparisons, which were the aim of this study.

Weight in activity models

For models investigating age-related variation in activity patterns, I weighted the duration of the tracking period to control for shorter observation periods due to logger failure. To estimate the appropriate weighting scheme for each activity metric, I iteratively truncated complete tracks in monthly increments, and, for each increasing length of observation time, I calculated the difference from the median of the whole tracking period. I investigated the effect of several transformations (square-root, $\log_e$ and $\log_{10}$) on the relationship between this measure of error due to incomplete sampling and the length of tracking period. In the models, I selected $\log_{10}$ of the number of days of tracking as it resulted in a linear decrease in error with time.

Monthly changes in activity patterns

I investigated changes in activity patterns across the non-breeding period with age using linear mixed effects models (LMM). The number of landings and hours spent in flight were modelled from monthly individual medians of consecutive light and dark periods to control for seasonal variation in the duration of daylight and darkness. Month was included as a continuous predictor variable up to the third-order polynomial and age was a categorical variable with three levels: young (6 – 14 years), middle-aged (14 – 24 years) and old-aged (25+ years).

Table A4.1. Sample sizes for analyses of age-related variation.

			Type of analysis		
Year	Status	Sex	Spatial (full)	Activity	Stable isotopes*
2008	Successful	Male	22	5	13 (36)
		Female	15	8	6 (18)
	Failed	Male	3	2	3 (9)
		Female	3	2	4 (10)
2009	Successful	Male	15	12	9 (23)
		Female	21	18	14 (41)
	Failed	Male	3	2	0 (0)
		Female	0	0	0 (0)
			82	49	48 (137)

*The number of individuals is given; where there were multiple samples per individual, the total number of samples is also shown in parentheses. Status denotes previous breeding outcome: successful = individuals that bred in the previous year; failed = individuals that failed to raise an egg during the year of tracking. The activity dataset is smaller than the spatial dataset as many loggers failed to successfully record immersion data. *****For some individuals it was not possible to collect three feathers and so the number of samples does not always multiply by three.*

Table A4.2. Model selection table for generalized linear models (GLM) examining the relationship between age and breeding success for all monitored breeding wandering albatrosses at Bird Island.

Year	Sex	N	Predictor variables		
			Null	Age	Age + Age^2
2009	Female	610	5.18	0.00	0.11
	Male	631	0.00	2.01	3.65
2010	Female	529	5.14	4.29	0.00
	Male	573	2.19	4.19	0.00

Models were run separately for males and females in the 2009 and 2010 breeding seasons corresponding to geolocator tracking conducted in previous non-breeding seasons 2008 and 2009. AIC values are shown for models without the effect of age (Null), the linear effect of age (Age) and both the linear and quadratic effect of age (Age + Age2), and the best models are shown in bold. N = number of individuals.

Table A4.3. Observed and randomized spatial overlap (utilization distribution overlap index, UDOI) across the whole utilization distribution (UD) of wandering albatrosses, compared between age classes for both sexes combined, between sexes for all ages combined and between years for all ages and both sexes combined.

Class	Observed	Randomized	*P*
Age (both sexes)	–	–	–
Young *vs.* middle-aged	1.90	2.00 ± 0.11	0.16
Middle- *vs.* old-aged	2.15	1.97 ± 0.18	0.93
Young vs. old-aged	1.97	1.84 ± 0.21	0.85
Sex (all ages)	1.63	2.20 ± 0.11	< 0.001
Year (all ages and sexes)	2.06	2.14 ± 0.10	0.17

Young = 6 – 14 years; Middle-aged = 14 – 24 years; old-aged = 25+ years. Randomized overlaps are shown as a median ± interquartile range. P represents the proportion of randomized overlaps that were smaller than the observed.

Table A4.4. Observed and randomized spatial overlap (Bhattacharyya's affinity, BA) of core (50%) and general use (95%) utilization distributions (UDs) of wandering albatrosses, compared between age classes for each sex.

	50%			95%		
Class	Observed	Randomized	*P*	Observed	Randomized	*P*
Male	–	–	–	–	–	–
Y vs. M	0.38	0.39 ± 0.03	0.30	0.86	0.85 ± 0.02	0.71
M vs. O	0.32	0.34 ± 0.05	0.27	0.79	0.78 ± 0.05	0.66
Y vs. O	0.28	0.32 ± 0.06	0.18	0.76	0.78 ± 0.05	0.29
Female	–	–	–	–	–	–
Y vs. M	0.35	0.37 ± 0.03	0.21	0.79	0.84 ± 0.04	0.10
M vs. O	0.36	0.36 ± 0.04	0.48	0.78	0.81 ± 0.04	0.22
Y vs. O	0.34	0.37 ± 0.04	0.19	0.74	0.78 ± 0.13	0.13

Young (Y) = 6 – 14 years; Middle-aged (M) = 14 – 24 years; old-aged (O) = 25+ years. Randomized overlaps are shown as a median ± interquartile range. P represents the proportion of randomized overlaps that were smaller than the observed.

Table A4.5. Summary of the top five generalized linear mixed models (GLMM) examining the change in activity patterns of wandering albatrosses tracked with geolocators by age and month, including the random effect of individual bird identity

Age	Month	Month^2	Month^3	d.f.	logLik	AICc	ΔAICc	Weight
Number of landings per day								
X	X	X	X	8	-814.4	1645.1	0.0	0.72
–	X	X	X	6	-817.4	1647.0	1.9	0.28
X	X	X	–	7	-856.0	1726.2	81.1	0.00
–	X	X	–	5	-858.9	1727.9	82.8	0.00
X	X	–	–	7	-871.0	1756.3	111.2	0.00
Hours spent dry per day								
X	X	X	X	8	-1190.4	2397.0	0.0	0.68
–	X	X	X	6	-1193.2	2398.5	1.5	0.32
X	X	X	–	7	-1205.5	2425.3	28.3	0.00
–	X	X	–	5	-1208.3	2426.7	29.7	0.00
X	X	–	X	7	-1217.0	2448.2	51.2	0.00

The most parsimonious model is shown in bold. X = predictor variables retained; – = predictor variables not retained in the model; d.f. = degrees of freedom; logLik = log-likelihood of model; AICc = Akaike information criterion corrected for small sample sizes; ΔAICc = change in AICc from most parsimonious model; Weight = Akaike weight given to that model.

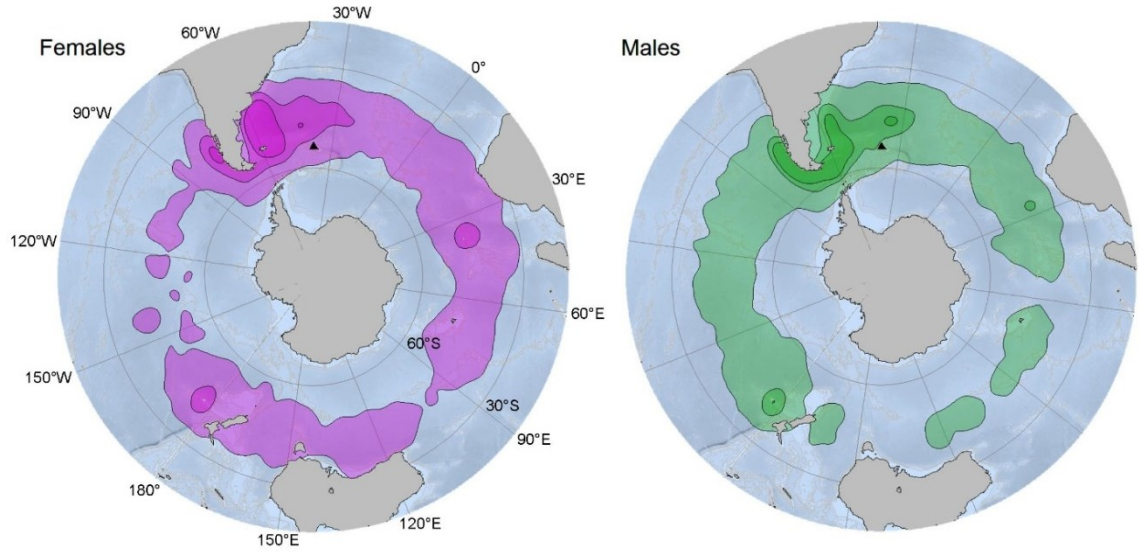

Figure A4.1. Sex differences in core (25% and 50%) and general use (95%) utilization distributions (UDs) of female (*n* = 36) and male (*n* = 35) wandering albatrosses tracked with geolocators from Bird Island (black triangle) during non-breeding.

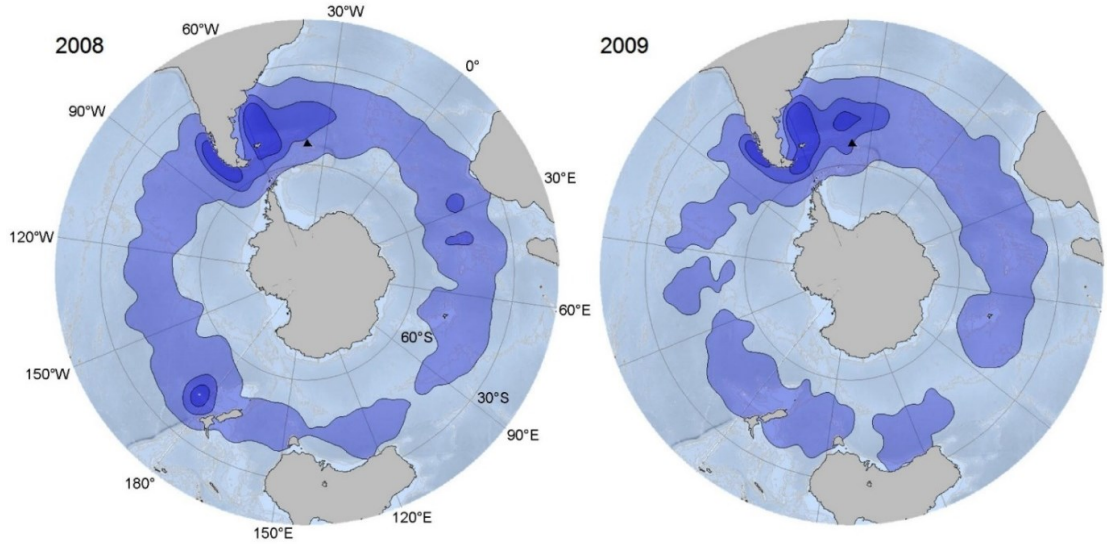

Figure A4.2. The core (25% and 50%) and general use (95%) utilization distributions (UD) of non-breeding wandering albatrosses tracked with geolocators from Bird Island (black triangle) in 2008 (n = 43) and 2009 (n = 38).

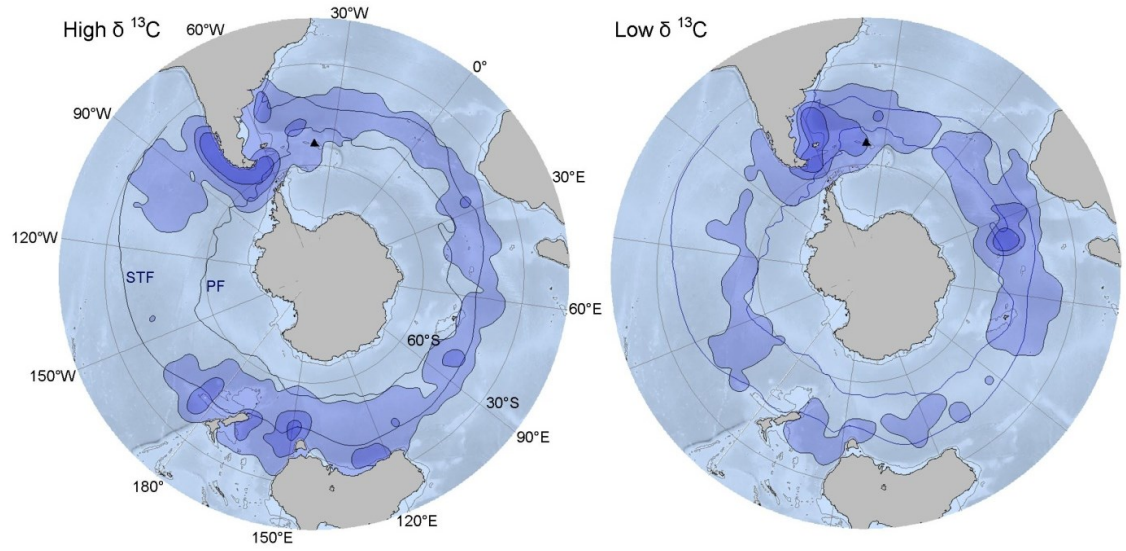

Figure A4.3. The core (25% and 50%) and general use (95%) utilization distributions (UD) of non-breeding wandering albatrosses tracked with geolocators from Bird Island (black triangle) that have high (> -17 ‰, n = 6, ages 21 – 25) and low (< -19 ‰, n = 6, ages 21 – 33) average values of δ ^{13}C from body feathers. The annual positions of the Polar (PF) and Subtropical Fronts (STF) are shown by dark-blue lines and 1,000 m isobaths by dark-grey lines.

APPENDIX 5 – SUPPLEMENTARY MATERIAL FOR CHAPTER 6

Methods

Resighting probability

Birds that were tracked as fledglings were from an intensive study area, where chicks are fitted with plastic rings with a unique character code, and as a result are more likely to be resighted at the colony than birds with only metal rings. The probability of resighting of tracked birds was also likely to be higher because of the need to retrieve and redeploy loggers. Immatures prospect the colony for variable periods in the first few months of the breeding season (Pickering 1989), and may not be observed. In contrast, as all nests on the island are marked and visited multiple times to determine the identity of the partners, breeding birds have a very high probability of being detected unless they fail early in incubation.

Tracking details

Geolocator data were filtered to remove unrealistic flights speeds of >40 kmh^{-1} sustained over a 48 h period (Phillips et al., 2004b). Sea-surface temperature correction is known to reduce errors associated with light-based locations (Shaffer et al., 2005); however, as the loggers deployed in the early years of the study did not record temperature, I did not use this approach, to avoid a bias in latitude estimates by age. Loggers tested for saltwater immersion every 3 s; MK4–5 and MK14 loggers stored the sum of positive tests at the end of each 10 min period providing a value ranging from 0 (continuously dry) to 200 (continuously wet), and MK7 loggers recorded the time of every transition from wet to dry and vice versa that lasted ≥ 6 s. In order to standardise the resolution, data from MK7 loggers were resampled to match those of the other logger types.

Migratory schedules

Dates of arrival and departure at the colony were determined using a combination of immersion and location data. In some years, due to memory limitations, loggers recorded light but not activity data during the latter part of the deployment. For each individual year, I calculated arrival and departure based on location, (whether the bird

was within 500 km of the colony; Guilford et al. 2009), and activity data, (long dry periods spent on land). For individuals where the arrival dates were calculated separately from both activity and location data, the two were highly correlated (Spearman's rank correlation = 0.94, S = 518, $P < 0.001$), so I chose to use dates derived from location data due to the larger sample size.

Home range analysis

Due to logger battery failure or logistical constraints, individuals were not always tracked for the whole year. For years with complete coverage, I calculated the change in area of 50% and 95% UDs with increasing month and plotted the relationship (Fig. A5.1). The size of the home range area reached a plateau at c. 7 months, particularly for the 50% UD, and so this was used as the minimum cut-off for subsequent analyses.

Nearest neighbour distances

I calculated distances between tracks using least cost paths in the package *geoGraph* in R (Jombart et al. 2013); geographic area is modelled by a rectangular grid, where each node has a set of spatial coordinates and a set of attributes which can be used as habitat descriptors with movement modelled as paths through connected nodes. While the world database contains 40,000 nodes, distances between neighbouring nodes, although equidistant, is not specified. I investigated the average distance between two nodes by creating a 10° x 10° grid in the South Atlantic, and calculated distances between pairs of nodes using great circle distances in the R package *field*s (Nychka et al. 2016). The mean distance between two nodes was 109 ± 18 km, less than the error of geolocation (Phillips et al. 2004); this value was therefore used as the scaling factor in NND analyses. Sea-ice was defined as areas of > 15% coverage over the period 1981-2010, based on data obtained from the National Snow and Ice Data Center (http://nsidc.org/data/g02135) (Fetterer et al. 2002, updated 2015). Sea-ice climatologies were integrated as cost layers and linked to the relevant month of tracking data to control for seasonality in sea-ice concentration throughout the year.

Analyses of individual consistency

For these analyses, I only considered data from immatures to reduce potential differences between life stages (see results). I used a resampling approach similar to that adopted to predict sample sizes in Chapter 2, to determine the influence of the number of years of tracking on spatial consistency. For each individual with 5+ years of data, I calculated the average value of spatial overlap for an increasing number of years, selected at random 100 times, without replacement. The median value for each individual and number of year combinations is plotted in Figure A5.2. Among-individual differences in the average within-individual overlap were largely maintained regardless of how many years that individual was sampled. However, I chose 3 years of tracking as a minimum cut-off as overlap scores largely stabilised thereafter (Fig. A5.2).

Results

Tracking details

Of the 58 individuals tracked as fledglings in 2001, 28 (48%) returned to the colony and were resighted for the first time in 2004–2010, and one was found dead on a beach in New Zealand and its logger subsequently returned. Loggers were still attached to 24 of those 28 birds, of which 18 (31% of the total deployed) provided data. Of these, 17 loggers yielded more than one week of data, 15 had lasted for at least 6 months, and 4 for at least a year and a half (Fig. 6.1). As a result, there were no data on the third and fourth years at sea. From 2006-2008, 20 of the 28 birds that returned to the colony were tracked as immatures for up to 8 years, until the study ended in 2013; however, tracking of individuals was discontinuous because of logistical constraints or logger battery failure. Over the course of the study, 15 birds were tracked in 2002, 4 in 2003, 13 in 2006, 8 in 2007, 10 in 2008, 10 in 2009, 12 in 2010, 9 in 2011, 4 in 2012 and 3 in 2013, providing a total of 88 years of data from 22 individuals (Fig. 6.1). By 2015, 14 birds (64%) had recruited into the breeding population, and tracking data were obtained for 3 individuals as non-breeding adults, including one individual for two years. Five birds (23%) did not survive to 2015 (Fig. 6.1); one was killed by a longline vessel and 3 were presumed dead as they were not resighted at the colony in the last 5 years. On average birds were tracked for 4 ± 2 years (n = 22), including for 3 ± 2 years (n = 19) as immatures.

Resighting probability

Chicks fitted with loggers were more likely to be resighted at the colony as an immature or adult than others in the 2001 cohort (tagged juveniles: 48%, n = 28; non-tagged juveniles: 27%, n = 151; ΔAIC = -9.00, χ_1^2 = 11.01, *P* = <0.001), and were resighted at a significantly younger age (tagged: 5.4 ± 1.1 years, non-tagged: 9.9 ± 2.2 years; ΔAIC = -85.90, χ_1^2 = 482.79, *P* = <0.001).

Table A5.1. Parameter estimates of linear mixed-effects models investigating ontogenetic changes in the activity patterns of wandering albatrosses tracked with geolocators during their first year post-fledging, and in their first eleven years. Parameter estimates are from models shown in Table 1.

Response variable	Time period	Parameter coefficients				
		Intercept	SexM	Age	Age2	Age3
Time in flight (%)	Yr 1	0.57 (0.50 – 0.64)	–	0.10 (0.055 – 0.14)	-0.015 (-0.022 – -0.0072)	0.00069 (0.00030 – 0.0011)
	All yrs	0.87 (0.83 – 0.92)	–	-0.0097 (-0.013 – -0.0064)	–	–
Time in flight daylight (%)	Yr 1	0.42 (0.32 – 0.53)	–	0.28 (0.21 – 0.34)	-0.041 (-0.052 – -0.029)	0.0018 (0.0012 – 0.0024)
	All yrs	0.93 (0.86 – 1.00)	–	-0.017 (-0.022 – -0.012)	–	–
Time in flight darkness (%)	Yr 1	0.10 (-0.0065 – 0.21)	–	0.10 (0.039 – 0.17)	-0.0022 (-0.014 – 0.0094)	-0.00032 (-0.00092 – 0.00026)
	All yrs	0.55 (0.50 – 0.60)	-0.084 (-0.14 – -0.025)	–	–	–
No. landings hr-1	Yr 1	0.40 (0.38 – 0.43)	–	-0.0033 (-0.0065 – -0.0000084)	–	–
	All yrs	0.42 (0.38 – 0.46)	–	-0.043 (-0.071 – -0.0016)	0.0059 (0.00035 – 0.0012)	-0.00028 (0.00060 – 0.000035)

No. landings hr-1 light	Yr 1	0.47 (0.40 – 0.54)	–	0.023 (0.0019 – 0.044)	-0.0022 (-0.0037 – -0.0070)	–
	All yrs	0.81 (-0.87 – -0.75)	–	-0.026 (-0.034 – -0.019)	–	–
No. landings hr-1 dark	Yr 1	0.49 (0.41 – 0.57)	–	-0.013 (-0.056 – 0.0029)	0.0051 (-0.0019 – 0.012)	-0.00034 (-0.00069 – -0.0000077)
	All yrs	0.49 (0.48 – 0.51)	-0.033 (-0.048 – -0.017)	-0.0062 (-0.0083 – -0.0041)	–	–
Wet bout length light (hrs)	Yr 1	0.54 (0.015 – 1.28)	–	-0.71 (-1.11 – -0.32)	0.12 (0.050 – 0.19)	-0.0054 (-0.088 – -0.0019)
	All yrs	-0.39 (-0.71 – -0.054)	–	0.079 (0.060 – 0.098)	–	–
Wet bout length dark (hrs)	Yr 1	2.17 (1.86 – 2.48)	–	-0.41 (-0.51 – -0.31)	0.025 (0.018 – 0.033)	–
	All yrs	1.94 (1.66 – 2.22)	0.53 (0.29 – 0.77)	0.038 (0.0053 – 0.070)	–	–

Model coefficients are shown with 95% confidence intervals from the minimal adequate models in parentheses. – = not kept in most the parsimonious model.

Table A5.2. Results of linear mixed-effects models investigating ontogenetic changes in the activity patterns of wandering albatrosses tracked with geolocators during their first year post-fledging, and in their first eleven years. Total values per day are shown rather than proportions in Table A5.1.

Time period	Response variable	N	Predictor variables					df	AICc	ΔAICc	R^2 marginal	R^2 conditional
			Age	Age^2	Age^3	Sex	Month					
First year	Time in flight (hrs)	12 (125)	X	X	X	–	n\a	6	500.6	1.01*	0.22	0.36
	Time in flight daylight (hrs)	12 (125)	X	X	X	–	n\a	6	450.9	1.14*	0.27	0.43
	Time in flight darkness (hrs)	12 (125)	X	X	X	–	n\a	6	99.2	0.00	0.63	0.77
	No. landings	12 (110)	X	–	–	–	n\a	4	375.9	0.69*	0.04	0.22
	No. landings light	12 (110)	X	X	X	–	n\a	6	326.8	0.00	0.33	0.51
	No. landings dark	12 (110)	X	X	X	–	n\a	6	-29.4	0.00	0.48	0.64
All years	Time in flight (hrs)	14 (58)	X	–	–	–	X	15	2070.5	0.65*	0.23	0.25
	Time in flight daylight (hrs)	14 (58)	X	–	–	–	X	15	374.0	0.00	0.38	0.40
	Time in flight darkness (hrs)	14 (58)	–	–	–	X	–	4	1740.3	0.00	0.05	0.10
	No. landings	14 (58)	X	X	X	–	X	17	1383.6	1.43*	0.31	0.34
	No. landings light	14 (58)	X	–	–	–	X	15	-70.8	0.23*	0.46	0.47
	No. landings dark	14 (58)	X	X	X	X	X	18	81.1	0.00	0.30	0.30

For further explanation, see Table 1 in main text.

Table A5.3. Results of the top five linear mixed effects models investigating ontogenetic changes in the arrival and departure dates of immature wandering albatrosses tracked with geolocators.

Response	Predictor variables				df	AICc	ΔAICc
	Age	Age^2	Age^3	Sex			
Departure date	X	X	–	–	5	683.0	0.00
	X	X	X	–	6	683.2	0.23
	X	X	–	X	6	684.7	1.77
	X	X	X	X	7	685.0	2.06
	X	–	–	–	4	697.7	14.81
Arrival date	X	–	–	–	4	13.1	0.00
	X	X	–	–	5	14.6	1.51
	X	X	X	–	6	15.3	2.26
	X	–	–	X	5	15.4	2.29
	X	X	–	X	6	17.0	3.92

The best supported model is shown in bold. X = predictors retained; – = predictors that were not retained;

Table A5.4. Model selection tables determining the shape of the age function for the size of core areas of wandering albatrosses tracked with geolocators. Top model (with lowest AIC) is shown in bold. The model number indicates the age at which a breakpoint occurs; Age = linear effect of age; - = no effect of age.

Size of 50% UD		
Model	AICc	ΔAICc
2	313.75	0.00
Age	324.46	10.71
8	327.06	13.31
-	327.16	13.41
9	327.77	14.02
3	328.12	14.37
4	328.12	14.37
5	328.12	14.37
7	328.52	14.77
6	328.83	15.07
10	329.25	15.49
11	329.33	15.58

Table A5.5. Parameter estimates of linear mixed-effects models investigating ontogenetic changes in the area of home ranges and spatial consistency of wandering albatrosses tracked with geolocators.

	Response	Parameter coefficients		
		Intercept	Yr_{diff}	Age
Area of home ranges				
	50% UD	2.99 (2.55 – 3.47)	n\a	1.90 (1.00 – 2.76)*
	95% UD	18.77 (16.34 – 21.29)	n\a	–
Spatial consistency				
Yr_{Paired}	50% UD	0.23 (0.19 – 0.28)	n\a	–
	95% UD	0.61 (0.51 – 0.70)	n\a	–
	NND	2786 (1932 – 3785)	n\a	–
Yr_{All}	50% UD	0.35 (0.23 – 0.48)	-0.071 (-0.11 – -	0.043 (0.0035 –
	95% UD	0.47 (0.34 – 0.60)	-0.077 (-0.11 – -	0.055 (0.014 – 0.096)
	NND	5775 (4553 – 7169)	–	-96 (-159 – -48)

See Table 2 in main text for details on models. Model coefficients are shown with 95% confidence intervals from the minimal adequate models in parentheses. – = not kept in most parsimonious model; n\a = not included in model.

Table A5.6. Model selection tables determining the shape of the age function for metrics of spatial consistency in wandering albatrosses tracked with geolocators. The top model (with lowest AIC) is shown in bold. Age = linear effect of age; - = no effect of age.

50% UD			95% UD			NND		
Model	AICc	ΔAICc	Model	AICc	ΔAICc	Model	AICc	ΔAICc
Age	**-185.89**	**0.00**	**Age**	**-168.74**	**0.00**	**Age**	**0.00**	**1436.54**
11	-185.66	0.24	2	-167.86	0.89	3	10.26	1446.80
10	-184.39	1.50	11	-167.86	0.89	4	10.26	1446.80
7	-184.22	1.68	10	-166.19	2.55	5	10.26	1446.80
6	-184.17	1.72	3	165.20	3.55	2	16.15	1452.69
2	-183.56	2.34	4	165.20	3.55	11	21.48	1458.02
-	-183.46	2.44	5	-165.20	3.55	10	28.42	1464.96
3	-183.43	2.47	-	-163.99	4.76	6	33.61	1470.15
4	-183.43	2.47	8	-163.87	4.88	7	38.10	1474.64
5	-183.43	2.47	6	-163.84	4.90	-	38.42	1474.97
8	-181.99	3.90	7	-162.26	6.48	8	40.45	1476.99
9	-181.46	4.44	9	-162.08	6.67	9	40.48	1477.02

Table A5.7. Observed and randomized spatial overlap (Bhattacharyya's affinity, BA) of core (50%) and general use (95%) utilization distributions (UDs) and nearest neighbour distances (in km) of individual wandering albatrosses tracked with geolocators as immatures. Randomized overlaps are shown as a median ± interquartile range. *P* is the proportion of randomized overlaps that were smaller than the observed.

Id	No. years	Overlap of core areas			Overlap of general use areas			Nearest neighbour distances		
		Observed	Randomized	P	Observed	Randomized	P	Observed	Randomized	P
16	4	0.29	0.11 ± 0.05	< 0.001	0.77	0.40 ± 0.09	< 0.001	1,627	4,686 ± 1,032	< 0.001
23	7	0.15	0.10 ± 0.03	0.007	0.55	0.37 ± 0.05	< 0.001	2,240	4,398 ± 597	< 0.001
24	8	0.18	0.11 ± 0.02	< 0.001	0.49	0.38 ± 0.05	< 0.001	3,363	4,294 ± 543	0.01
26	3	0.18	0.10 ± 0.06	0.06	0.54	0.37 ± 0.15	0.06	2,523	4,360 ± 1,726	0.06
30	5	0.20	0.12 ± 0.04	0.004	0.46	0.41 ± 0.06	0.2	5,199	4,365 ± 803	0.9
32	3	0.23	0.15 ± 0.07	0.06	0.51	0.44 ± 0.11	0.2	4,996	4,377 ± 1,439	0.7
43	3	0.09	0.07 ± 0.07	0.4	0.34	0.34 ± 0.15	0.5	4,138	4,920 ± 1,733	0.3
44	4	0.19	0.15 ± 0.05	0.1	0.59	0.44 ± 0.08	0.003	2,470	4,195 ± 1,115	0.005
45	4	0.26	0.07 ± 0.07	< 0.001	0.75	0.33 ± 0.15	< 0.001	1,449	4,942 ± 1,853	< 0.001
47	6	0.27	0.11 ± 0.03	< 0.001	0.68	0.39 ± 0.12	< 0.001	2,209	4,622 ± 709	< 0.001
50	3	0.17	0.10 ±0.07	0.1	0.59	0.38 ± 0.12	0.004	1,283	4,809 ± 1,572	< 0.001
51	3	0.19	0.10 ± 0.07	0.06	0.63	0.37 ± 0.16	0.009	1,754	4,413 ± 1,799	0.004
63	3	0.05	0.12 ± 0.04	1.0	0.20	0.39 ± 0.07	1.0	5,421	4,465 ± 879	0.9
75	4	0.28	0.13 ± 0.05	< 0.001	0.74	0.43 ± 0.10	< 0.001	1,064	3,497 ± 1,093	< 0.001

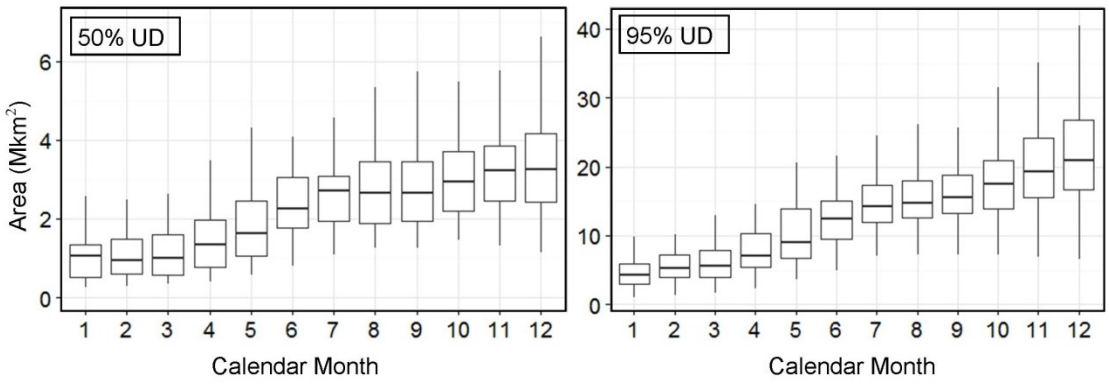

Figure A5.1. The area of core (50%) and general use (95%) utilization distributions (UDs) of wandering albatrosses tracked with geolocators in relation to the number of months of tracking, for all individual years where there was full tracking coverage. Area was calculated for each individual year in monthly increments.

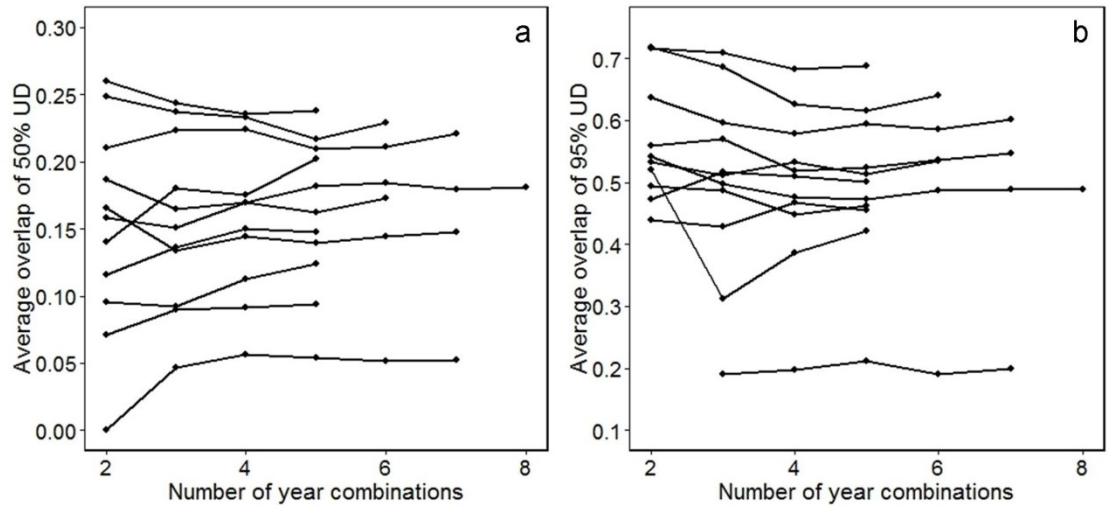

Figure A5.2. The relationship between number of years of tracking and average spatial overlap of core (50%) and general use (95%) utilization distributions (UDs) for 11 individual wandering albatrosses tracked with geolocators with 5+ years of data, each shown with a black line. The median value for each number of year combinations is shown.

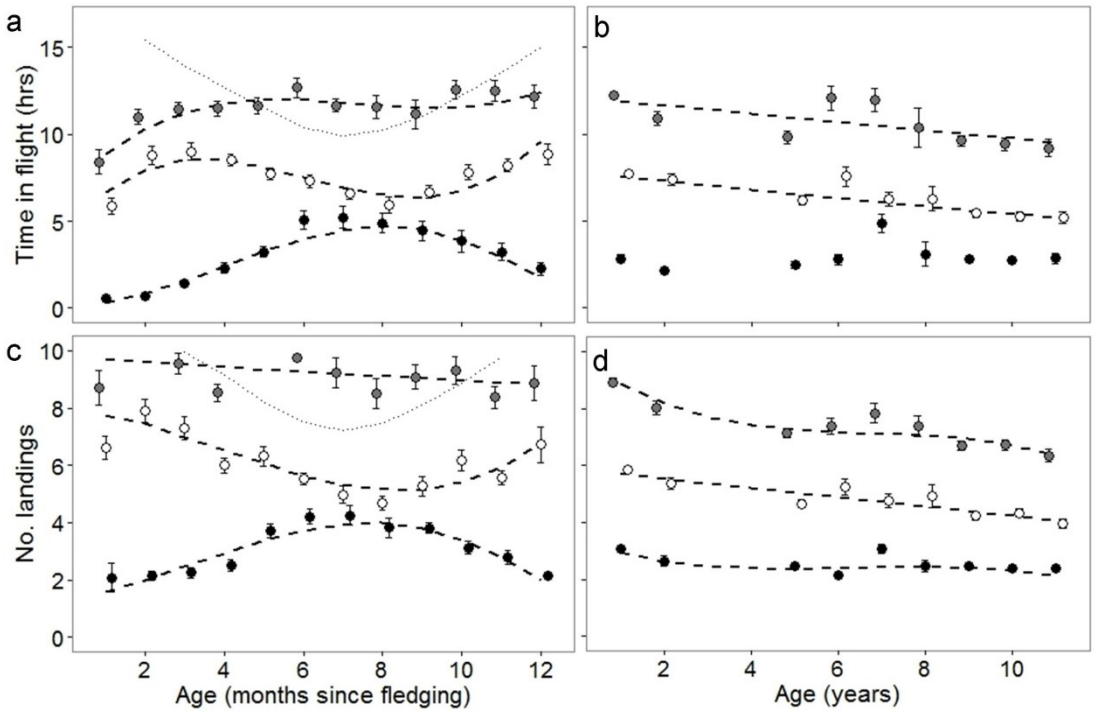

Figure A5.3. Ontogenetic changes within individuals in the (a-b) flight (time spent flying per day) and (c-d) foraging activity (number of landings per day) of wandering albatrosses tracked with geolocators during the first year (a and c) and across all years (b and d). See Figure 3 for details. The average number of hours of daylight is shown as a dotted line in plots (a) and (c).

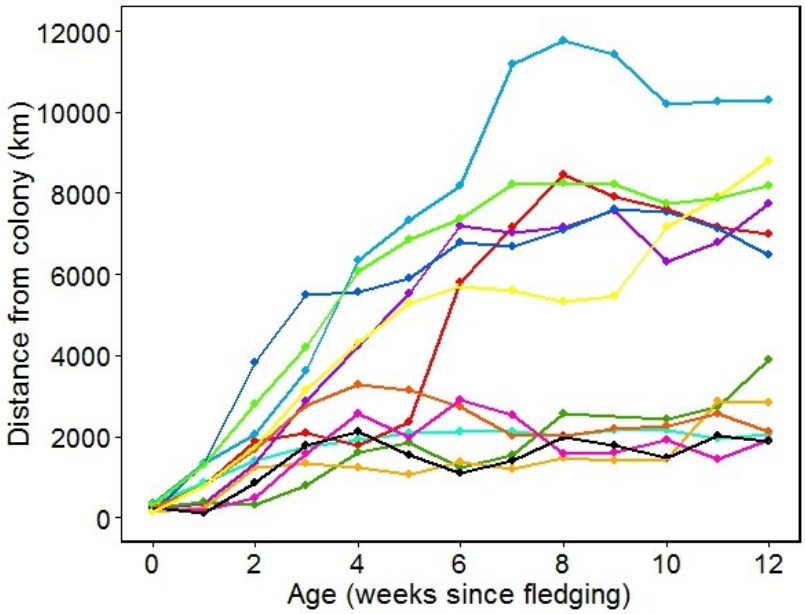

Figure A5.4. Juvenile dispersal of wandering albatrosses in the first 3 months post-fledging. The 12 individuals from Figure 2 are shown in the same colours, except here black replaces white. Distances are shown as weekly means.

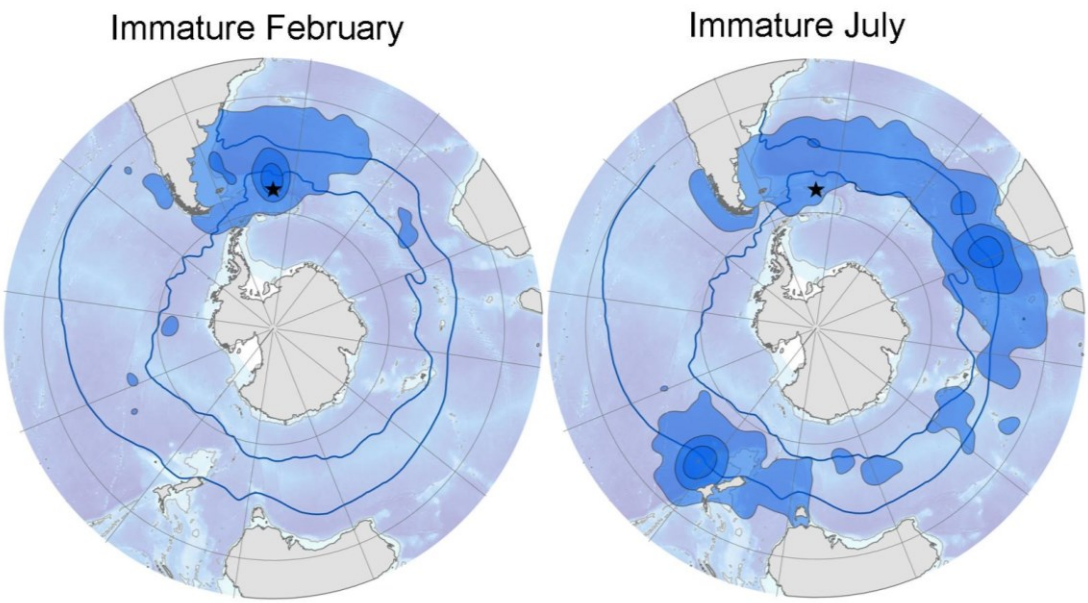

Figure A5.5. The core (25% and 50%) and general use (95%) utilization distributions (UDs) of immature wandering albatrosses tracked with geolocators from Bird Island, South Georgia (black star) in February (n = 63) and July (n = 67). The average positions of the Subtropical and Polar Fronts are shown with dark-blue lines.

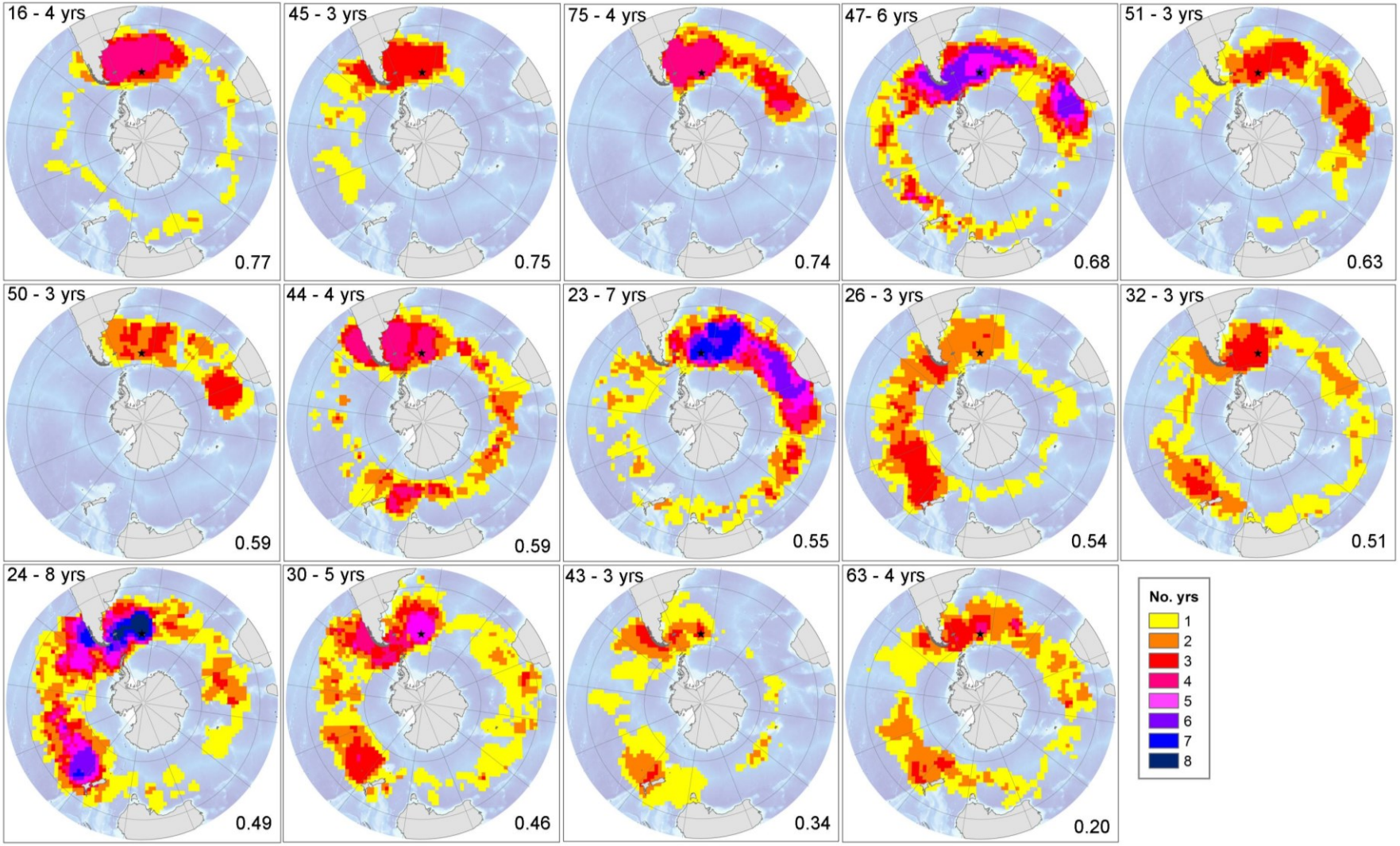
16 - 4 yrs
0.77
45 - 3 yrs
0.75
75 - 4 yrs
0.74
47- 6 yrs
0.68
51 - 3 yrs
0.63
50 - 3 yrs
0.59
44 - 4 yrs
0.59
23 - 7 yrs
0.55
26 - 3 yrs
0.54
32 - 3 yrs
0.51
24 - 8 yrs
0.49
30 - 5 yrs
0.46
43 - 3 yrs
0.34
63 - 4 yrs
0.20
No. yrs
1
2
3
4
5
6
7
8

Figure A5.6. The general use (95% UD) distributions of 14 individual wandering albatrosses tracked for 3–8 years as immatures. The overlap index score (Bhattacharyya's affinity, BA) is shown for each individual in the bottom right of each plot, with higher numbers indicating greater spatial overlap.

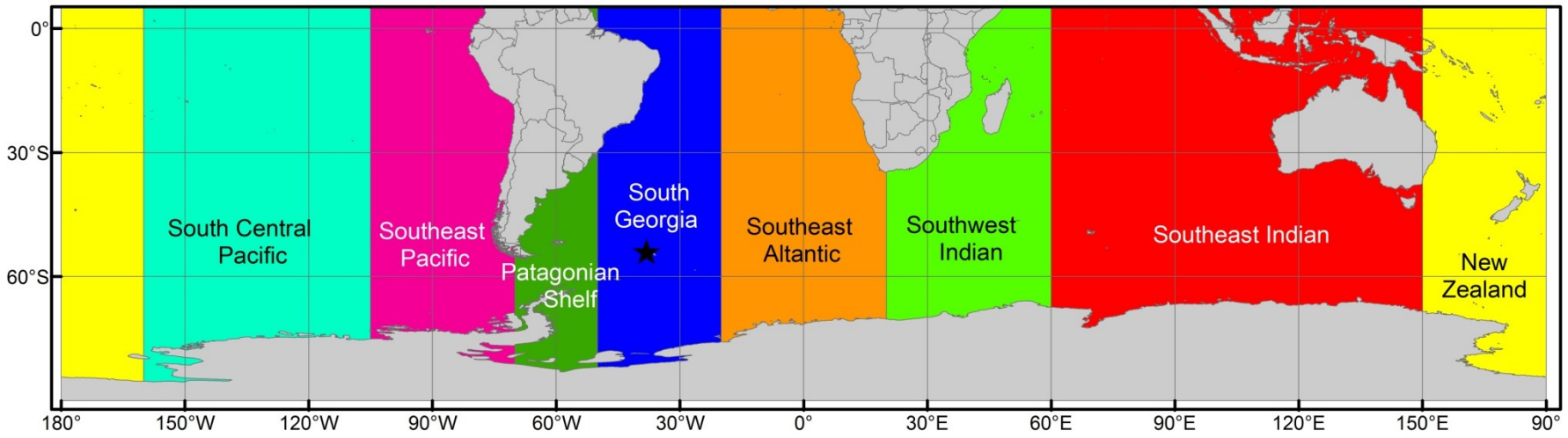

Figure S7. Visual representation of the eight sectors shown by different colours in Figure 9, based on longitude: New Zealand (150°E - 160°W), South Central Pacific Ocean (160°W - 105°W), Southeast Pacific Ocean (105°W - 70°W), Patagonian Shelf and Falkland Islands (70°W - 50°W), South Georgia (50°W - 20°W), Southeast Atlantic Ocean (20°W - 20°E), Southwest Indian Ocean (20°E – 60°E) and the Southeast Indian Ocean (60°E - 150°